STUDIES IN BARLEY BREEDING

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SUMMARY

Part I

An experiment was conducted to investigate the inheritance of, inter alia, the traits days to heading, productive tiller number, grains per ear and 1000 corn weight in a spring barley population.

A diallel cross arrangement was used and the experiment involved thirteen parents, four of which were 6-rowed varieties, and the F_1 and F_2 progeny derived from all possible crosses between them.

The experiment was conducted in two successive seasons and in each season two independent blocks were sown with plants individually randomized within each block at a spacing of 15 cm x 7.5 cm.

Computer programs were written and the data were analysed using the facilities at the Edinburgh Regional Computing Centre.

Although the inheritance of the trait days to heading was found to be largely due to additive genetic effects, partial dominance was also detected generally operating towards earlier heading. This was particularly clear for the 6-rowed genotypes. In the population as a whole gene asymmetry was detected and there was an excess of recessive genes. Large effects for general and specific combining ability both for early and late heading were detected.

In the analyses of data for the main yield components it was shown that considerable non-additive

genetic variance was operating and dominance was generally found to be acting towards higher expression of the respective trait. Heterosis was detected and epistasis occurred in crosses between 2-rowed and 6-rowed genotypes for 1000 corn weight.

Broad and narrow-sense heritabilities were estimated for the three traits and it was shown that in the 2-rowed material narrow-sense heritability was low for the trait productive tiller number, rather higher for the trait grains per ear and fairly high for the trait 1000 corn weight.

General and specific combining ability estimates were computed and were considered useful guides in the choice of parents.

Genotypic, phenotypic and environmental correlation coefficients between the four traits were computed.

Part II

Canonical analysis was applied to data from the diallel experiment grown in the second season. Several of the conclusions drawn from the biometrical analyses were confirmed and useful information was obtained as to the degree of resemblance between genotypes in terms of the traits analysed.

Canonical analysis was also used in a selection experiment conducted on a composite cross population of spring barley. The method provided a means of selection which gave heavy weighting to those traits which, regard-

less of their relative economic values, allowed good discrimination between lines. Several lines were selected which, in small-plot yield trials, performed well relative to control varieties.

CONTENTS

CHAPTER I

GENERAL INTRODUCTION

In contrast to the genus Triticum, which consists of a polyploid series of species in which there are diploid, tetraploid and hexaploid representatives, the section Cerealia Ands., which comprises the grain producers of the genus Hordeum, contains no polyploid representatives. The development of the barley crop has been entirely at the diploid level and hybridization and mutation have occurred without the development of cytological or genetical barriers (Bell, 1951). An account of the phylogeny and evolutionary development of the cultivated barleys is given in Appendix I.

BARLEY IMPROVEMENT IN THE U.K.

Until the middle of the nineteenth century most of the cultivated barley populations consisted of mixtures of many types and in some parts of the country these mixtures resulted in aggregates which were recognisably distinct from other such aggregates. Examples are "Scotch Common", a hardy barley with a short growing period and grown in N.E.Scotland, and "Old Irish", grown in some parts of Ireland. Beaven (1947) refers to such populations as "local varieties" and in Germany the term "Landgerste" (the barley of the land) was used.

Improvements were made by selecting individual plants within these local varieties and multiplying

their progeny. This, together with improvements in seed handling which reduced the tendency for stocks to become mixed, gradually led to the appearance of more or less pure lines. Not only were lines produced which were particularly well adapted to local areas but they were relatively uniform in quality and this suited the maltsters.

From about 1835 the variety Chevallier, named after its introducer the Rev. Dr John Chevallier, began to assume a leading position amongst varieties in the British Isles. This variety arose from the progeny of a few selected ears and up to 1886 (Beaven, loc cit), 80% - 90% of the barley grown in England was of this variety. From the date of its introduction until about 1900, Chevallier occupied an important position as a malting barley in Britain and on the Continent, and malting competitions were regularly won by the variety up to 1914. Chevallier, however, suffered from the defect of having long, somewhat weak straw, and with the increasing fertility of the arable land resulting from the greater use of artificial fertilizers, this defect became more evident (Hunter and Leake,1933). The higher yielding, but poorer quality Archer barley had stiffer straw and was generally favoured where lodging was a serious problem. Archer barley was a mixture of types derived from the old common English narrow-eared barley.

In the early 1890's the variety Spratt was grown quite widely in the Fen districts and E.S.Beaven made several selections of different lines of this stiff-strawed variety, one of which was multiplied and sent to the Irish Department of Agriculture. From this barley came the Spratt parent of Spratt-Archer bred by Dr H.Hunter in Ireland from the cross Spratt x Archer. This variety, although similar in ear shape to the Archer parent, was superior in yield, stiffer-strawed, earlier in ripening, and of better malting quality (Hunter and Leake, loc cit).

During the first quarter of this century the variety Goldthorpe was a valuable malting barley but gave low yields relative to Archer, due partly to the tendency for the straw to become very brittle when ripe leading to ear losses before harvest. In an attempt to obviate this defect Beaven, in 1905, crossed Plumage, a form of Goldthorpe, with Archer and obtained a broad-eared form, very similar to Archer in straw characteristics, which he named Plumage-Archer. Seed stocks of both Spratt-Archer and Plumage-Archer were distributed throughout the seed trade in 1914 and these varieties dominated British barley acreages for the next thirty years, though the seed stocks were changed when improved forms were selected (Whitehouse, 1968). Writing in about 1940, Beaven (loc cit) remarked that 85% of the acreage of barley grown at that time was the progeny of four

plants only, three of which had been selected in his Warminster nursery. The four varieties were Spratt-Archer (42%), Plumage-Archer (28%), Plumage (10%) and Golden Archer (5%).

Beaven felt that the results of Mendel, publicised at the beginning of the century, were of limited application in plant breeding because of the large number of characters for which segregation would occur after hybridization, though he did concede that Mendel's work had led to more systematic methods of selecting individuals resulting from cross-fertilization.

In the introduction to his book, "Barley: Fifty Years of Observation and Experiment", Beaven wrote, ".... it may be agreed that we have to start with single plant cultures and then go on year after year selecting individuals from these cultures for the characters which we require, so that all our plants shall have a known pedigree. ... Without the single-plant culture method the results of Mendel and his successors could not have been established, but it is to the application of this method rather than to any Mendelian theories of unit characters and segregation that we must still look for further improvement on the value of our agricultural crops."

In the 1930's Bell, working at Cambridge, made a series of crosses between the well-tried British varieties and a number of recent introductions from Scandinavia. The most important of these crosses,

that between Plumage-Archer and Kenia, led to the selection of Proctor which was released for the 1953 season, twenty years after the original cross, and displaced virtually all the varieties previously grown.

Proctor remained the dominant spring barley variety for many years and is still (in 1973) on the Recommended List of the National Institute of Agricultural Botany, though the British spring barley acreage is now dominated by varieties bred in Holland and Scandinavia. Maris Otter, selected at the Plant Breeding Institute, Cambridge, from a cross between Proctor and the winter-hardy variety Pioneer, and released in 1965, is, however, widely grown as a winter barley.

The production and dissemination of new varieties is of immense importance to cereal production. F.R. Horne (1961) estimated that something like half the total improvement in cereal crops may be directly attributable to the use of new and better varieties. Royalties are now payable on new varieties. The Financial Times (quoted in Agricultural Merchant, Oct. 1966) stated that, "by the time a new variety is offered to farmers it will have cost its breeder anything from £20 000 to £50 000 and involved a fantastic gamble in the process". For a really successful variety, returns might reach well over £100 000 a year (Britton, 1969).

BREEDING METHODS

Techniques for handling hybrid populations

As has been seen, the early improvments were made by selecting phenotypically attractive plants from mixed populations, whereas in the last fifty years, apart from programmes designed to introduce single characters, such as disease resistance into otherwise desirable varieties, the majority of barley breeding programmes have involved hybridization followed by selection according to one of a few well-tried systems. Amongst these, perhaps the most widely used has been the pedigree method of selection which involves the repeated and detailed selection of individual plants throughout the early generations until the desired degree of homozygosity is attained, usually by the F_6 or F_7 generation. The most promising selections are then tested in small-scale yield trials from which further stocks can be multiplied. The method has been successfully used in the production of a large number of new varieties but it depends very much on the skill and experience of the plant breeder in the early stages of selection. Such evaluation by eye is, of course, of limited value for quality traits such as protein content or malting quality.

Particularly valuable where a single breeder must handle material from a large number of crosses, is the bulk method of selection. Following

hybridization the progeny are grown as unselected bulk for a number of years until the population consists of more or less homozygous individuals. During this time many of the less desirable genotypes may be eliminated by natural selection though there is evidence that desirable genotypes may compete poorly in a mixture and may also be eliminated. Selection at about F_4 will produce a number of more or less true-breeding lines which can be multiplied for field trials.

Lupton and Whitehouse (1957) described two selection systems which allow yield trials to be used at an earlier stage than is normally the case when the pedigree selection method is used. The first of these is known as the F_2 progeny method in which selection is carried out in the F_2 and the more promising F_3 selections are taken forward to yield trials in F_4, F_5 and F_6 without further selection within progenies. After this, single plant selections are again taken from the more promising lines. The alternative method described was the pedigree-trial method of selection in which selection is carried out on a single plant basis in each generation as in the pedigree system. In the F_4 generation single plants are selected from the better families for continued pedigree selection and within each of these families the remaining plants are bulked to give grain for a yield trial in the following year.

This process is repeated in F_5 and F_6. In this way it is possible to obtain yield estimates from F_5 onwards without breaking the continuity of the pedigree selection.

The methods outlined above have also been described by Bell and Lupton (1962). An extreme example of the use of the bulk method of selection was described by Dros (1957) for the breeding of two spring barleys, Vada and Minerva. In this case selection was started on the hybrid population twenty years after the cross had been made. Vada is one of the Dutch varieties at present recommended by the N.I.A.B. as a general purpose spring barley for farmers in Britain.

Composite Cross Populations

An extension of the bulk method of breeding has been practised by barley breeders in California who created composite cross populations by intercrossing a large number of genotypes and bulking the progeny. These genetically diverse populations were then multiplied and maintained for many generations of selfing, with only a small amount of natural crossing, under natural selective forces. It is claimed that population fitness improves with successive generations and that yields may eventually approach those of breeders' improved varieties. Further details of the work on composite cross populations are given in Appendix II.

A variety resulting from this evolution-based method might be a superior population or a pure line selected at some intermediate stage in the evolution of the population. Suneson (1956) suggested that conventional selection might be practised after about fifteen generations of natural selection.

Clearly, the method is slow but it should perhaps be regarded as a kind of investment in genetic variability. Populations with a wide genetic base can be set up and maintained almost indefinitely with very little effort. Natural crossing, although perhaps of low frequency, would ensure the slow release of genetic variability, and inclusion in the population of a male-sterile line would further facilitate genetic recombination.

The use of composite populations in barley has not been widespread, perhaps because breeders have not the patience for handling them. The Californian breeders can certainly claim some success however, for in 1956 J.R.Harlan was able to list nineteen important varieties derived from composite crosses.

The rapid reduction of genetic variability appears to be a universal concomitant of the advancement of agriculture (Harlan,1956) and the reduction of variability resulting from the methods commonly used by plant breeders is beginning to cause concern (Bennett, 1965; Frankel,1950; Simmonds,1962,

1968; Walker, 1969). Walker pointed out that most plant breeders encourage and participate in the accumulation of germ plasm whilst at the same time using methods aimed at reducing genetic variability at the fastest possible rate. The concept of composite cross populations offers the opportunity to fully utilize variability which might otherwise only be available to the breeder in the form of a museum collection. Traditionally such collections are regarded as sources of "characters", generally oligogenic, which are simply transferred to locally adapted genotypes by back-crossing (Simmonds, loc cit). Since the object of a back-crossing programme is to transfer as little foreign genetic material as possible to the recipient, only a trivial enrichment of genetic variability is achieved. The incorporation of material from such a collection into composite cross populations should allow more comprehensive utilization and, indeed, further generation of genetic variability.

F_1 hybrid barleys

The increased yield and vigour which may be achieved by exploiting heterosis in crops such as maize and onions is well known, and although generally exploited in allogamous crops, similar advantages of heterosis have been found in autogamous crops.

Interest in the possibility of producing hybrid cereals on a commercial scale was stimulated by the discovery of the cyto~~genetic~~plasmic male-sterility - restorer system in wheat. The basis of male-sterility as exploited in barley is different from the wheat system: it is not cytoplasmic but ~~genetic~~nuclear. The first gene for male-sterility in barley was found by Suneson in 1936 and since that date perhaps fifty more genes have been found. All these male-sterility genes are simply inherited and are recessive in their expression.

The demand for hybrid barley will ultimately depend on the magnitude of the heterotic effect which must, in this context, be defined as the superiority of the F_1 over the better parent and, indeed, over the best variety currently available. The superiority may be in yield in a specific environment or in stability of yield performance over a number of environments.

Most of the evidence for heterosis in barley comes from spaced plant trials, thus Weinhues (1968) showed that particular crosses involving a line with good general combining ability gave yields 18-21% higher than the better parent when plants were grown in rows 20 cm apart and at 5 cm spacing within the rows. Again, Hayes(1965) studied forty-five F_1 hybrids from a diallel cross involving ten parents adapted for growing in Western Europe. Rows

were spaced at 38 cm with 15 cm between plants. The F_1 generation showed an average increase of 10% in yield over the parents but only two hybrids significantly outyielded their better parent. In another experiment, reported by the same author, parents and hybrids were grown at 10 cm intervals in rows 15 cm apart. Average F_1 values were significantly different from the means of the parents in only the characters weight per grain and secondary tiller production. Under the closely spaced conditions of the normal drilled crop, superiority in the production of secondary tillers is unlikely to have a significant effect on yield.

Rasmussen (quoted by Hayes, 1968) found that superiority of the F_1 hybrids relative to the mid-parent value at a wide spacing (22.5 cm) was greater than that at a close spacing (2.5 cm). At the close spacing the best hybrid was not equal to the highest yielding variety but at the wider spacing it was much superior.

To set against the apparent over-estimation of hybrid advantage resulting from spaced planting is the likelihood of F_1 seed being lower in kernel weight than that of the parent because of the clipping of the florets either for artificial pollination or to facilitate natural cross-pollination. The production of hybrid seed on a commercial scale would, of course, have to be independent of any

such artificial aids to facilitate crossing.

Turning to the economics of hybrid seed production, two factors are of prime importance. One is the additional cost of hybrid seed, the other is the increase in income expected from the additional yields. Whereas in corn and sorghum in the United States the ratio of harvested to planted seed is around 350:1, the ratio in barley and wheat is about 27:1 (Rasmusson, 1966). This figure is about right for barley in the U.K., so that the margin is relatively narrow and the balance between seed costs and the yield advantages, associated with hybrid seed, which the farmer can expect at his particular level of production may be a delicate one.

The choice of parents - prediction

The choice of parents in a hybridization programme is a matter of considerable importance to the plant breeder. If he is considering improvement in one particular trait a knowledge of the mode of inheritance will be of some importance and for this he may draw on the results of experiments using models developed for the estimation of genetic variances. Several experimental designs have been designed for this purpose and have in general evolved by the adoption and subsequent extension of crossing designs traditionally used by breeders. Five such designs were described and evaluated by Kearsey (1965), who concluded that of the five designs he evaluated,

the half diallel cross was to be preferred, though he cautioned that the small number of parents usually used may be unrepresentative of the population as a whole.

Applications of the diallel technique, which is described in Appendix IV, to self-pollinating cereals have been described by Whitehouse *et al* (1958), Lupton (1961), Crumpacker and Allard (1962) working on wheat and by Johnson and Aksel (1959) and Hayes (*loc cit*) working on barley. All these authors attempted to make predictions about the performance of particular crosses in the subsequent generations. Whitehouse *et al* confined their attention to yield trials in F_1 and F_2 and thus could not confirm their predictions. Lupton, however, grew trials at F_3 and F_4 and was able to say, "... the crosses which show the greatest promise in subsequent generations have in each case been noted in the trials in F_1 and F_2, although in certain cases, crosses noted in this trial have not maintained their promise in later generations".

Crumpacker and Allard (*loc cit*), measuring heading date in wheat, used parental and F_1 data to predict segregation in F_2 and certain other generations. Two procedures were used in comparing predictions and observations. First, the observed phenotypic variances of different F_2 populations were ranked in order of magnitude and compared with the rankings predicted

from the diallel analysis. Second, observed frequency distributions were compared with the frequency distributions predicted from information provided by the diallel analysis on the major genes differentiating the parents. Three major genes were suggested by the analysis of parents and F_1 and segregation at F_2 agreed fairly well with postulations for two of these genes but evidence for the third gene was not confirmed. These authors also used W/V graphical analysis (Jinks, 1954) to estimate the means of the theoretically top dominant and bottom recessive parents. They found that the near-top dominant and the near-bottom recessive genotypes were present among the ten parents used and concluded that the limits of selection had already been reached.

Johnson and Aksel (loc cit) used a scaling test and selected three crosses on the basis of F_1 and F_2 performance on the grounds that they were consistently high yielding and showed complementary gene interaction.

Such examples do not illustrate prediction in the sense of deciding which parents to cross but rather of deciding, after analysis of the early generations, which crosses are likely to yield the most valuable segregates in later generations. Information from genetic analyses can, of course, be used in the decision of which parents to use if the breeder can be reasonably sure that the sample of parents used

in the experiment is representative of the population from which he is to draw, but unless his sample is a large one and chosen at random, this may not be the case.

In consideration of complex traits such as yield it has been recognised that much of the complexity may be resolved by partitioning the character into its sub-units. Biometrical resolution has sometimes shown the components of yield to be under simpler control than total yield (Walker,1969; Whitehouse et al, 1958). In addition, attempts have been made (Lupton et al, 1967; Lupton,1969; Lupton,1972; Bingham,1971) to relate physiological traits and growth parameters to yield in wheat. Genetical analysis of such physiological traits as are found to be important in determining yield in barley may lay the basis for prediction of suitable parental combinations. However, Lupton et al (loc cit), in a study of five wheat varieties and a random selection of hybrids between them, found that although the varieties differed signficantly for the growth parameters measured, and that some of these parameters were generally associated with yield, variability between seasons and between crosses was such that doubt was cast on the possibility of making useful predictions of valuable parental combinations.

Multiple objectives

Experienced plant breeders will generally have a mental picture of the ideal selection in terms of a number of important traits. Three main methods of selection are available: tandem selection, where the desired level for one trait is achieved before selection is commenced for the next; independent culling levels in which levels are set for each trait, and rejection or selection practised on each independently; index selection where a total score of merit is composed from contributions from each trait. Tandem selection has been shown (Hazel and Lush,1942; Young,1961; Pesek and Baker,1969a,b) to be far less efficient than index selection. Correlations between characters involved may drastically affect the frequency of alleles necessary for the successful continuance of a tandem programme (Walker, 1969). Independent culling levels suffers from the possible existence of negative genetic correlations between traits apart from the fact that the order of selection of the traits will clearly be important. Index selection (Smith,1936) involves the use of discriminant functions. In the derivation of a selection index each trait is given a weighting which will depend upon (1) the phenotypic variances and covariances between each of the characters involved; (2) the genotypic variances and covariances; (3) the relative economic values of the several traits

(Robinson, Comstock and Harvey, 1951).

A quite different approach to the analysis of multivariate data in plant breeding has been proposed by Whitehouse (1970 a, b). This involves the use of canonical variate analysis. The analysis is lengthy and could not be reasonably undertaken unless a computer was available, but this is becoming less and less of a problem and today plant breeders with a minimum of programming knowledge can make use of an increasing number of software packages.

CONCLUSIONS

In spite of an almost static situation at the beginning of the century barley breeding has progressed extremely rapidly. The so-called "traditional methods" of pedigree selection, involving repeated and detailed selection of individual plants of a hybrid population throughout the early generations, have been enormously successful. This technique depends very much on the skill and experience of the plant breeder and many plant breeders who have utilized traditional methods, albeit with success, for some time might confess to occasionally wondering whether their approach is "scientific" enough. The practise of crossing the best with the best and hoping for the best may not owe much to the science of genetics but it seems to have been effective and in the hands of a connoisseur of the

crop it may equal if not exceed the efficiency of a scientifically based selection method.

However, the facts are rather daunting. Traditional plant breeding methods involving crossing and back-crossing may be adequate when there are only a few gene differences between the parents used in a cross, but when there are many gene differences population size becomes limiting. As the number of segregating allelic pairs becomes larger, the number of possible genotypes increases rapidly, so that, for example, for parents differing by twenty-one allelic pairs the number of possible genotypes in the F_2 is $3^{21} = 1.045 \times 10^{10}$. Obviously a plant breeder must work within the limitations of available land and labour so that, in order to plan his programme efficiently, he should know the genetic limitations too. Hence a knowledge of the nature of the inheritance of important traits and an idea of the number of genes or effective factors involved should determine which parents he should cross and the size of his early generation populations.

It could be argued that in screening a population at F_2 and F_3 or, in the case of a composite population, F_{15} to F_{20}, by visual assessment, the breeder is applying a method similar to that of independent culling levels. A line may be eliminated on the grounds of excessive height, or of low resistance to disease - each criterion being applied

independently of any others. There may well be an order of priority in the breeder's mind but there may be a tendency to eliminate heavily on characters which are easily assessed at first glance. Valuable material may be lost unless a method of quantifying each character and giving it a weighting is used. On the other hand the sheer labour of recording the observations will reduce the population size which can be handled.

The situation can perhaps be summed up by quoting from a paper given at the First International Barley Genetics Symposium in Wageningen, 1963 by Dr G.D.H. Bell. "There is of course, room for differences of opinion on the most appropriate methods and techniques, not only as general procedures, but with regard to specific objectives in individual circumstances. There should however, be cogent reasons, based on scientific knowledge, for the use of different methods and techniques, and also some agreement in scientific opinion on the correct procedures. It must be admitted that the breeder is faced with rather too much speculation, rather than confident prediction, in coming to important decisions, although all imaginative research work must have a speculative element. In plant breeding it has to be admitted some of the most spectacular contributions in the improvement of varieties have not been accurately predicted, and the present

situation has not greatly changed in that the unpredictable still occurs." (Bell, 1964).

CHAPTER 2

INTRODUCTION TO THE WORK DESCRIBED IN THE THESIS

I Biometrical studies

Amongst the most useful to the plant breeder of the biometrical techniques now available is the diallel analysis, details of which are given in appendix IV. The analysis was used in the work described here to study the inheritance principally of yield components, though an analysis of time to heading was also performed (Riggs and Hayter,1972) and is submitted as part of this thesis.

The analysis of a complex character, which is expressed as a product of a number of component characters, may be complicated by interactions at the genetic level or simply because of the multiplicative nature of the character. Thus, if two varieties have 'yields' of 100 composed of three components 2.0 x 1.4 x 35.7 and 1.2 x 2.2 x 37.9 then the F_1, assuming that the components are additive, will have a yield of 1.6 x 1.8 x 36.8 which is 6 per cent higher than the parents (Whitehouse 1968). Williams (1959) using examples from tomato and wheat observed, "In wheat as in the tomato, an essentially additive genetic system conditions a multiplicative somatic basis to yield which, when analysed as a simple character, leads erroneously to a non-additive genetic interpretation."

Griffing (1956) described combining ability analyses for the two assumptions in which the genotypes are assumed to be (1) a random sample from a population, and (2) a chosen or fixed set. In the first situation the genotypic effects are considered random variables and in the second they are considered constants. In practice the parents chosen for diallel crossing are generally, as in this work, a fixed set and, strictly speaking, the experimental material must be regarded as the population about which inferences are to be made. This situation has been designated model I by Eisenhart (1947). The objectives, as far as the analysis for combining ability is concerned, are to compare the combining abilities of the parents themselves and to identify the most promising combinations. Kempthorne (1956) in a critical discussion of the theory of the diallel cross, questioned the value of estimating additive variance, dominance variance and so on, unless the estimated quantities are measures of the characteristics of a definite population. The estimates can have relevance only to a particular population and will not be constant from population to population.

It must be said that there is today a growing realization that little further progress is likely to be made by elaboration and sophistication of the biometrical techniques which have predominated in the field of quantitative genetics. The actual

genetic architecture of traits can only be approached in a statistical sense and with various assumptions (Lee and Parsons, 1968). Indeed, doubts as to the usefulness of the techniques are not new. Gilbert (1958), whilst conceding that further knowledge of the genetics of continuous variation in general would be beneficial to all plant breeding, expressed doubt as to how the "polygene" analysis could help the plant breeder in a specific problem since, ".... even accepting the genetical assumptions and statistical methods employed, it is not known which plants contain which genes." The genetical assumptions (Hayman 1954) implicit in diallel analysis have been attacked both by Gilbert (loc cit) and by Kempthorne (loc cit).

Notwithstanding such criticism, however, it was felt by the writer that, in setting up a pedigree breeding programme from the very beginning, useful information as well as hybrid material might be obtained by adopting the diallel cross technique.

II Studies involving multivariate analysis

Multivariate statistical analyses have been widely used in the fields of psychology, sociology, archaeology and biology. In biological studies multivariate techniques have been used as an aid to discrimination between species or between environments

with respect to one or more species (see Blackith and Reyment, 1971 for examples.) Namkoong (1966) reported the use of principal component and canonical correlation analyses in a study of introgression in pine. Hashiguchi and Morishima (1969) described a method for estimating the genetic contributions of principal components to individual variates measured in rice, and Holland (1969) described the use of component analysis as an aid to the interpretation of data.

Applications of multivariate techniques in plant breeding have, until recently been somewhat infrequent though multivariate data have been used in the construction of selection indices (Smith, 1936; Henderson, 1963) and a vector analysis has been proposed by Grafius (1963, 1964, 1965) by which populations with means close to an ideal might be constructed. Recently, a number of workers (e.g. Perkins, 1972; Shukla, 1972) have considered the application of multivariate techniques in the elucidation and interpretation of the genotype-environment interaction. Krzanowski (1972) described a number of techniques which, when applied to multivariate data, effectively reduce the dimensionality without loss of information.

Whitehouse (1970 a,b) proposed the use of canonical analysis as a method of predicting promising

parental combinations and of comparing the performance of crosses relative to an ideal or model variety. In the first paper on this subject results were described for the analysis of a diallel cross between eight barley genotypes on which six traits had been measured. A scatter diagram was presented to show the relative positions of points representing the parents, and distances between the points in multi-dimensional space were calculated. It was shown that in general the points representing hybrids fell near the mid-point between the parents. This suggested an essentially additive system for the inheritance of the variates measured. This was also the conclusion when each trait was analysed individually by the W/V analysis of Jinks (1956). No analysis was possible on F_1 data because of severe lodging and the results described were for the F_2 and F_3 generations in which large effects of dominance and epistasis might not be expected.

The analysis of a second barley diallel was described in the later paper. In this case data were available for seven traits measured on the parents and F_3 generation. The average deviation of the points representing hybrids from their mid-parental positions was 35 per cent of the parental distance. This deviation was attributed to the integrated effects of dominance and epistasis but

was considered sufficiently small to allow the mid-parental points to be used as guides to the cross positions.

It was suggested that the breeder could define his breeding target by including in the analysis actual data from an existing control variety or concocted data representing an ideal or model selection in terms of the traits under analysis. It should then be possible, by reference to a scatter diagram and to a chart of distances, to judge which crosses fell closest to the ideal or which genotypes might be most likely, when crossed, to yield hybrids close to the ideal.

Crosses showing large deviations from the mid-parental points might be further studied since the deviation might be an indication of non-additive gene systems which could be of use to the breeder. The elucidation of such effects, however, might entail a biometrical analysis of each trait individually.

Data from the diallel experiments described in Part I of this thesis were analysed by this method in order to investigate relationships between parents and their hybrids which may not have emerged clearly from the biometrical analyses, particularly with regard to the traits of importance in determining yield.

The principals underlying the application of canonical analysis to data from a set of genotypes and crosses between them, as outlined above, extend also to a situation where it is required to select the best lines from a population representing a mixture of pure lines. In this case, however, since it may be expected that a relatively large number of lines will be selected, it would be appropriate to define a target "area" rather than a point. Again, this might be done either by using several standard varieties or by constructing an ideal range which should, of course, be realistic both in terms of the inter-relationships between the traits under analysis and the potential of the population under selection.

In Chapter 7 an experiment is described in which this method of selection was applied to a composite population of spring barley.

PART I

BIOMETRICAL STUDIES

CHAPTER 3

CULTIVARS AND EXPERIMENTAL METHODS

The experiment was conducted in order to study a number of quantitatively inherited characters including yield and its components and the production of diastatic enzymes. The thirteen spring barley varieties used in the study are listed in Table 3-1. Most of the two-rowed varieties were, at the time of planning the experiment, of some commercial interest, whilst the six-rowed varieties, with the exception of Scotch Bere, were chosen for their high diastatic enzyme activity during germination. Scotch Bere was included as an adapted six-rowed variety which had not been subjected to selection for diastatic power.

Mating design

The original intention was to produce a full diallel set of 13^2 combinations with a target of 30 F_1 grains for each of the p^2 - p hybrid combinations. Because of rather poor conditions for crossing during the winter and also the inherently poor pollen production of some varieties, particularly Boreham Warrior, this target was not achieved.

The final arrangement consisted of a 9 x 9 mating block with parents and reciprocals and a 13 x 13 half diallel set which incorporated the 9 x 9 full diallel

material. In addition, F_2 seed was produced by selfing hybrid plants in the greenhouse and a 13 x 13 half diallel arrangement for F_2 was sown in the same trial in each season. The parents sown were common to both F_1 and F_2 diallel sets.

Hybridization

Plants were grown in a heated, lighted, greenhouse. Most of the hybridization was carried out under fluorescent tubes but more satisfactory seed set was found when these lights were replaced by high pressure sodium lamps.

Emasculation of spikes on plants chosen as female parents was performed when the awns were just visible above the flag-leaf sheath. Varieties differed slightly, however, in the optimum time for emasculation, relative to degree of emergence of the spike from the leaf sheath. This was easily learned from experience and corresponded to a stage 2 - 3 days before anthesis.

The flag-leaf sheath was split and peeled back and the florets were trimmed by cutting away the awns and about one-quarter of the length of glume and palea. With sharp-pointed forceps a slit was made in the side of each floret and the three anthers removed. Great care was taken to remove every anther as one anther remaining could result in accidental selfing. After emasculation the spike

was labelled with a jeweller's tag bearing the variety name and the date. A small cellophane bag was then placed over the spike, to prevent accidental out-crossing, until the stigmas were ready to be pollinated.

Spikes were removed from plants intended as male parents when the anthers were nearly ready to dehisce. On these spikes too, the florets were trimmed as for emasculation. If the spikes were at the right stage the anthers were extruded after a few minutes and were picked off with forceps. Emasculated spikes were usually ready for pollination 2 - 3 days after emasculation, when the stigmas were feathery in appearance and the florets were frequently gaping. Depending on conditions of humidity and temperature, the stigmas remained receptive for several days.

Each stigma was pollinated by dusting with a single anther from the male parent. After pollination the cellophane bag was replaced, the variety name of the pollen parent was written on the label together with the date, and the label then tied round the base of the cellophane bag.

Developing hybrid grains were usually visible 3 - 4 days after pollination.

Experimental Design

The trial was sown in each season as two

replicate blocks and each block constituted a separate and independent experiment. Considering a single block details of the design are given below.

a) Genetic material

Each cross in the 9 x 9 full diallel was represented by 5 individual plants and in the 13 x 13 half diallel by 10 individual plants. The 13 parents were also represented by 10 individuals, the first 5 individuals only of each parent being taken for the full diallel analysis. For the purpose of their inclusion in the F_1 half diallel, the reciprocal crosses of each parental combination in the full diallel were pooled to give 10 individuals per cross. This is shown diagramatically below.

Diallel cross arrangement and number of plants per cross

	1	2	3	4	5	6	7	8	9	10	11	12	13
1	10	5	5	5	5	5	5	5	5	10	10	10	10
2	5	10	5	5	5	5	5	5	5	10	10	10	10
3	5	5	10	5	5	5	5	5	5	10	10	10	10
4	5	5	5	10	5	5	5	5	5	10	10	10	10
5	5	5	5	5	10	5	5	5	5	10	10	10	10
6	5	5	5	5	5	10	5	5	5	10	10	10	10
7	5	5	5	5	5	5	10	5	5	10	10	10	10
8	5	5	5	5	5	5	5	10	5	10	10	10	10
9	5	5	5	5	5	5	5	5	10	10	10	10	10
10										10	10	10	10
11											10	10	10
12												10	10
13													10

b) Field layout

Each individual plant constituted a genotype replicate and was randomized amongst all the other plants from the time of sowing. The randomization was done with the aid of a computer after each plant had been allocated a treatment number, and a total of 1690 plants were grown in each block.

Each replicate block consisted of two sub-blocks of four rows each surrounded by two guard-rows which were sown with a single variety. The rows were set 15 cm apart with 7.5 cm between plants within rows.

Sowing

Rather than sowing seed directly into the ground, use was made of paper pots. These can be obtained in blocks, each block resembling a honeycomb (Paper pots No.B.213 ex S.A.I. Horticulture Ltd.). Each pot was 2 cm diameter by 12.5 cm long, and after soaking, could be separated from its neighbours and placed directly into a dibbed hole in the field. (Plate 1)

The seed was sown in dry soil, one per pot, according to the randomization previously prepared and a label, punched on aluminium Dymo tape, was pushed into the soil beside each seed. In addition to the trial material, approximately 5 grains of each cross were sown in separate sets of pots.

Plate 1. Seedlings in paper pots

Because the crossing technique used involved cutting off part of the lemma and palea before emasculation, the F_1 grains were partially naked. It was expected that these grains might imbibe water more quickly than grains resulting from natural selfing (parents and F_2's) and germinate more quickly. The normal grains were therefore chipped at the distal end to allow free imbibition of water.

Sowing such an experiment, with randomization of plants of different genotype is laborious and time-consuming and it was necessary to ensure that grain sown at the beginning of the operation did not begin to germinate before sowing was completed approximately two weeks later. Hence the pots were filled

with thoroughly dry soil and the whole experiment was watered after completion of sowing.

Guard-rows in the trial were sown directly in the field with a Planet hand-drill and this was done at approximately the time when the experimental material was watered. In the first season the variety Glacier was used and, in the second, Golden Promise. Both varieties are easily recogniseable in the field and both are very susceptible to mildew thus ensuring a good natural infection on the diallel material which could then be scored for severity of attack. In the first season, because of very dry conditions, the guard-rows had failed completely to braird by the time the diallel plants were dibbed out. A closer correspondence in growth was achieved in the second season.

The seedlings were transplanted in their pots when they were approximately 4" tall. Each aluminium label was transferred to the field with its respective plant. In the first season, white plastic labels were attached to the plants at harvest but in the second season, these labels were put on much earlier when the plants were scored for ear emergence.

In cases where no germination had occurred, replacements were made from the extra sowings made. Those replacement plants not immediately required were planted out in a separate block at the same

spacings (15 cm x 7.5 cm) as the experimental material.

Field diaries and notes for the experiments in both seasons are given in Appendix III.

Measurements and Observations

Field observations were made for mildew infection and time to heading. All other measurements were taken after the plants had been harvested.

Mildew (Erisyphe graminis f.sp.hordei)

This disease was more severe in Scotland in the 1970 season than usual and the experimental material became heavily infected when the plants were still quite young. The disease spread into the trial and the plants were assessed for their resistance to the disease using a system based on that given in the M.A.F.F. Guide (1970 and 1971). This was a subjective assessment of per cent leaf area covered by the fungus.

In the 1971 season the plants were older when infection occurred. Two assessments were made during the season and in addition, specimens were sent to the Pathology Department of the Cambridge Plant Breeding Institute, for race identification.

Days to heading

Plants were recorded for this character when 2 - 3 cm of the awns were visible above the flag-leaf of the main tiller. In the 1970 trial Block 2 was slightly behind Block 1 and the base dates

from which days to heading were recorded were May 26th for Block 1 and June 3rd for Block 2.

The 1971 trial was sown relatively earlier than the previous trial and heading of plants in both blocks was scored as days from May 1st.

Quantitative measurements

The plants were harvested on roots and the following measurements were taken in the laboratory:

plant height (cm),

tiller number (productive tillers only),

total ear length (sum of the lengths (cm) of all ears),

straw weight (g),

grain number,

grain weight (g).

Data handling

Data were recorded in each season on observation sheets printed according to the randomization of the field plan and the raw data were punched on cards, each card bearing the information from a single plant. The deck was stored in card-image form on magnetic tape at the Edinburgh Regional Computing Centre. A computer program was written by Mr J.L.Fyfe to assign each observation to its correct position in the mating design and to write the derandomized data for individual variates onto files held on disk at the E.R.C.C.

Five main computer programs were written by the author for the analysis of these data and are described below. The programs were written in the IMP Autocode language for use on the IBM and the ICL computers at the E.R.C.C.

LPBSO6J3

Computes (Wr,Vr) analysis of Jinks (1954). The program calculates the array totals, means and variances. Also, for each array, the covariance of the parents with their offspring in that array. The regression coefficient and standard error for the regression of array covariance (Wr) on array variance (Vr) and for the regression of Wr' on Wr are calculated.

Values are computed for parent total, parent mean, hybrid mean, variance of parents, (VOLO, in Hayman's (1954a) notation), mean variance of arrays (V1L1 for F_1), variance of array means (VOL1 for F_1) and mean covariance (WOLO1 for parents and F_1), and (Wr-Vr) for each array.

LPBSO6AB

Computes analysis of variance of the form:

Source	df	ss	ms
Blocks	b-1		
Genotypes	a-1		
Blocks x Genotypes	(b-1)(a-1)		
Within-fam.variance	ab(c-1)		

This program also computes the variance within each family and prints the variances in diallel form. A Bartlett's Test for homogeneity of the variances is performed and the value of chi-squared is printed.

LPBSO6H2

Computes analysis of variance of a full diallel table according to the method given by Hayman (1954b). The diallel table of mean values is given and the Hayman analysis for each block. Within-family variance is given for each block.

The analysis over blocks removes variance due to blocks and the variance ascribable to interactions with blocks of the main genetic components listed above. The average within family variances over blocks is also computed as in program LPBSO6AB.

LPBSO6H3

Computes analysis of variance of a half diallel, i.e. when reciprocal measurements are not taken or their differences assumed absent. The analysis is described by Jones (1965) using the same model as Hayman (1954b).

The print-out gives the half diallel table of mean values and the analysis and within-family variance for each block. The analysis over blocks removes the variance due to block differences and the variance ascribable to interactions with blocks of the additive and non-additive genetic components.

LPBSO6R7

Calculates least squares estimates for genetic components using the method of Mather and described by Mather and Jinks (1971). The analysis gives equal weight to all statistics and the same C - matrix is used for all experiments of the same design.

Data input is in free-field format and consists of a matrix of coefficients and a vector of statistics. Standard errors for the components can be calculated if there are more statistics available than parameters to be estimated.

Missing data

Inevitably in an experiment of this kind there were missing data due to the death of or accident to individual plants. A missing value in these data was represented as "999", a number unlikely to occur as a true value. All the programs were designed to discount missing values and to make the necessary reductions in the degrees of freedom.

CHAPTER 4

DIALLEL ANALYSIS OF THE MAJOR COMPONENTS OF YIELD

INTRODUCTION

It has been suggested by Grafius (1959), in a discussion of the phenomenon of heterosis due to epistasis, that a geometrical model can be envisaged in which yield (W) is the volume of a rectangular parallelipiped with edges X, Y and Z representing heads per plant, seeds per head, and average seed weight respectively. Assuming no positive correlation between the edges, different genes must affect each of them and there will be no genes for W per se. All changes in W will be due to the interaction of X, Y and Z or, in other words, to epistasis. Such interaction would be expected to disappear on transforming to a log scale. In a second paper, Grafius and Wiebe (1959) gave formulae which, depending on whether or not X, Y and Z are independent, show if it is better to select for increase in one edge alone or two edges or three edges in order to realise the greatest gain in volume or yield.

Whether or not genes determining yield as such exist, there is good reason to suppose that genetic analyses of the components of yield individually will throw more light on the inheritance of the complex character than analyses of yield itself (Whitehouse

et al, 1958; Grafius, 1959; Whitehouse, 1968; Thomas et al 1971a).

Perhaps the most comprehensive biometrical study of yielding capacity in barley yet attempted was that described by Johnson and Aksel (1959). Of the fifteen parents used in a diallel cross, ten were 6-rowed and five 2-rowed. The authors concluded that the component "grains per ear" was predominant in determining yield under the conditions obtaining in the experiment. In analyses of yield for the F_1 and F_2 these authors found evidence for over-dominance and there was an association between high yield and an excess of recessive genes. Similarly, high expression of each of the components of yield was generally associated with an excess of recessive genes and it was suggested that these components may simply represent different physiologically controlled expressions of the same genes (or effective factors).

Hayes (1965) described the results of detailed analyses of certain characters of importance in barley improvement in an investigation on the value of early generation trials in producing genetic information useful for developing improved cultivars of barley. Nevertheless relatively little published information is yet available, compared with the situation in wheat, regarding the quantitative characters of barley of commercial importance in N. W. Europe.

This chapter contains the results of a comprehensive genetic analysis of the major

components of yield for thirteen cultivars of barley and these results are discussed in Chapter 5.

RESULTS

Productive tiller number

The mean values for the thirteen parents are shown in table 4-1. Tillering was slightly higher in the second season but the range in both seasons was small.

The within-family variances were shown to be heterogeneous and this appeared to be largely due to the difference between the levels of variance in the 6-rowed and the 2-rowed material: the average variance for the F_1 of crosses between 6-rowed genotypes was approximately one-third of that for the F_1 of crosses between 2-rowed genotypes in both seasons whilst that for the F_2 of 6-rowed crosses was approximately one-half of that for 2-rowed crosses in both seasons. All analyses were conducted on untransformed data.

The analyses of variance (Hayman, 1954b) for the full and the half diallels are shown in tables 4-2 and 4-3 respectively. Both additive and non-additive genetic variance was shown to be operating in both seasons and in the 1971 data for the full diallel there was evidence of reciprocal effects ($\underline{d}$). The F_1 analysis for the full and the half diallels in 1971 showed a significant $\underline{b}_1$ item indicating differences between the mean hybrid performance and that of the parents. These differences were positive. No non-additive effects were detected in the analysis of the F_2 data for 1971.

TABLE 4-1

Tiller number (means of 10 plants) for 13 parent varieties in each two blocks and two seasons

		1970			1971		
		I	II	Mean	I	II	Mean
1.	Olli *	2.40	2.00	2.20	3.00	3.00	3.00
2.	Pirkka *	1.90	2.20	2.05	2.60	2.22	2.41
3.	Cambrinus	3.50	2.90	3.20	4.20	4.60	4.40
4.	Ymer	4.20	3.50	3.85	5.30	4.60	4.95
5.	Deba Abed	3.40	3.50	3.45	3.80	4.30	4.05
6.	Scotch Bere *	2.30	2.90	2.60	3.10	3.00	3.05
7.	O.A.C. 21 *	2.12	1.12	1.62	2.12	2.75	2.43
8.	Golden Promise	3.20	3.10	3.15	3.90	3.80	3.85
9.	Maris Baldric	4.20	3.30	3.75	3.80	3.90	3.85
10.	Midas	3.50	3.50	3.50	2.90	3.30	3.10
11.	Mosane	4.50	4.00	4.25	4.30	3.10	3.70
12.	Sultan	4.50	3.30	3.90	4.60	3.90	4.25
13.	Boreham Warrior	2.40	2.20	2.30	3.90	3.80	3.85
			±0.368	±0.260		±0.479	±0.339
	Mean	3.24	2.89		3.65	3.56	
			±0.102			±0.133	

* indicates 6-rowed parents

TABLE 4-2

Analyses of variance for tiller number in two seasons

Item	D.F.	9 x 9 F_1 1970 M.S.	9 x 9 F_1 1971 M.S.
a	8	31.060 ***	34.203 ***
b_1	1	0.598	11.188 *
b_2	8	0.792	0.779
b_3	27	2.740 ***	2.915 ***
b	36	2.247 ***	2.670 ***
c	8	1.165	2.487
d	28	1.175	2.370 ***
Blocks	1	52.645 ***	7.367
Ba	8	3.411 *	5.633 **
Bb_1	1	0.000	0.263
Bb_2	8	1.358	2.725
Bb_3	27	1.435	1.646
Bb	36	1.378	1.848
Bc	8	1.944	5.107 *
Bd	28	2.744 ***	1.253
Bt	80	2.116 ***	2.344 ***
Wfv		1.530 (634)	2.111 (643)

All effects tested against within-family variance

TABLE 4-3

Analyses of variance for tiller number in F_1 and F_2 for two seasons

		1970		1971	
		13 x 13 F_1	13 x 13 F_2	13 x 13 F_1	13 x 13 F_2
Item	D.F.	M.S.	M.S.	M.S.	M.S.
a	12	50.740 ***	38.099 ***	55.001 ***	32.220 ***
b_1	1	1.209	0.081	109.968 ***	3.875
b_2	12	2.787	3.965 **	3.262	3.990
b_3	65	2.812 ***	3.264 ***	4.696 ***	2.753
b	78	2.788 ***	3.331 ***	5.825 ***	2.958
Blocks	1	72.500 ***	93.022 ***	6.978	12.862 *
Ba	12	3.845 *	2.406	3.990	1.385
Bb_1	1	0.156	0.733	3.677	5.305
Bb_2	12	1.987	1.527	1.301	1.958
Bb_3	65	2.128	3.194 **	2.479	3.478 *
Bb	78	2.081	2.906 **	2.313	3.267 *
Bt	90	2.316 *	2.839 ***	2.537	3.016
Wfv (F_1 + P's)		1.805(1617 d.f.)		2.528(1631 d.f.)	

All effects tested against the within-family variance

TABLE 4-4

Analysis of variance for tiller number in the full diallel experiment over two seasons

Item	D.F.	M.S.
a	8	12.946 ***
b_1	1	1.696 **
b_2	8	0.162
b_3	27	0.614 ***
b	36	0.544 ***
c	8	0.619 **
d	28	0.306
Total (between families)	80	1.708 ***
Years	1	103.565 ***
Blocks (within years)	2	5.999 ***
Years x a	8	0.107
Years x b_1	1	0.661
Years x b_2	8	0.152
Years x b_3	27	0.516 ***
Years x b	36	0.440 ***
Years x c	8	0.112
Years x d	28	0.403 *
Years x Total	80	0.361 **
Block interactions	160	0.223

All effects tested against block interaction M.S.

TABLE 4-5

Analysis of variance for tiller number in the half diallel experiment over two seasons

Item	D.F.	13 x 13 F_1 M.S.	13 x 13 F_2 M.S.
a	12	10.249 ***	6.639 ***
b_1	1	6.715 ***	0.254
b_2	12	0.280	0.340
b_3	65	0.419 **	0.352 *
b	78	0.478 ***	0.349 *
Total (between families)	90	1.781 ***	1.187 ***
Years	1	106.763 ***	37.373 ***
Blocks (within years)	2	3.973 ***	5.294 ***
Years x a	12	0.330	0.396
Years x b_1	1	4.405 ***	0.141
Years x b_2	12	0.325	0.456 *
Years x b_3	65	0.332	0.250
Years x b	78	0.383 **	0.280
Years x Total	90	0.376 ***	0.296
Block interactions	180	0.243	0.293

All effects tested against block interaction M.S. for F_1 + parents

When analyses were conducted over seasons (tables 4-4 and 4-5) large seasonal differences were apparent and interactions between years and non-additive genetic variance were also detected. In the full diallel the $\underline{c}$ item was significant. The $\underline{b}_1$ item was also significant in the analysis for the F_1 half diallels and the significance of the Years x $\underline{b}_1$ interaction was not unexpected since this item was not statistically significant in the analysis of the 1970 data.

The regressions of Wr on Vr at F_1 were either not significantly different from zero or showed departures from unity. No significant differences between arrays for the values of Wr-Vr and Wr+Vr were detected in either season when these were tested against the corresponding differences over blocks (as below) except for the full diallel in 1970 when differences in Wr-Vr were significant at the 5 per cent level of probability.

The analysis of variance of the estimates of (Wr+Vr) and (Wr-Vr) for the 13 x 13 F_1 diallel set of crosses, 1970

Item	df	MS	F	
(Wr+Vr) Array differences	12	0.0845	1.55	N.S.
(Wr+Vr) Block differences	13	0.0546		
(Wr-Vr) Array differences	12	0.0124	<1	N.S.
(Wr-Vr) Block differences	13	0.0224		

In general regressions of Wr' on Wr gave slopes

of approximately one-half indicating equal gene frequencies.

Regression slopes for Wr on Vr and Wr' on Wr for the F_1 half diallels in both seasons are shown in figures 4-1, 4-2, 4-3 and 4-4. Analysis of the F_2 data generally resulted in non-significant regressions.

When the 2-rowed and the 6-rowed populations were analysed separately, significant regressions were found for the 6-rowed genotypes for both blocks in the 1970 data but only for block 1 in the 1971 data (figures 4-5 and 4-6). The Scotch Bere array occupied a position on the regression line indicating the presence of dominant genes in both seasons whilst the O.A.C. 21 array occupied the extreme recessive end of the line in both seasons.

Regressions obtained for the 2-rowed population were not significantly different from zero and the mean squares for the differences between arrays for the values of Wr-Vr and Wr+Vr did not reach significance when tested against their block interactions. Thus the poor regressions were apparently due to the absence of non-additive genetic variance rather than to interaction, though the true genetic effects may have been completely obscured by environmental effects.

The character appears from this analysis to be determined predominantly by additive effects at least in the 2-rowed genotypes and figure 4-1 shows a marked tendency for clustering of the points with the exception

Figure 4-1. Wr, Vr graph, F1 1970.

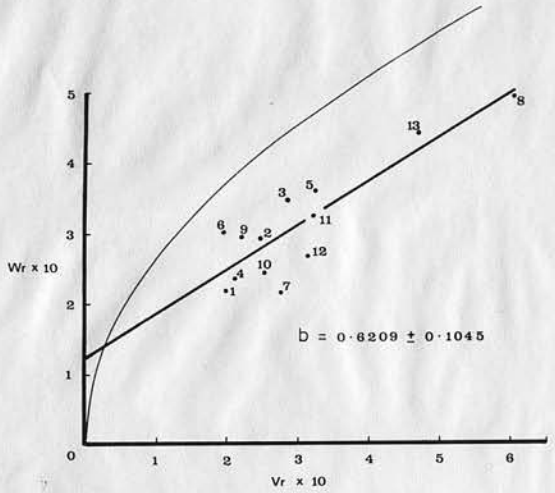


Figure 4-2. Wr', Wr graph, F1 1970.

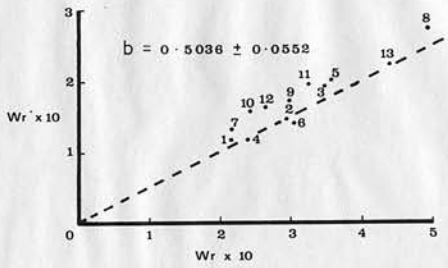


Figure 4-3. Wr, Vr graph, block 1, F1 1971.

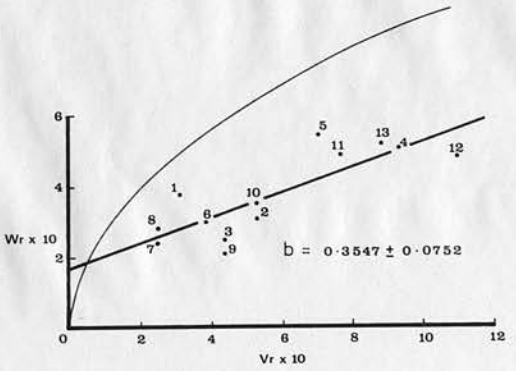


Figure 4-4. Wr', Wr graph, block 1, F1 1971.

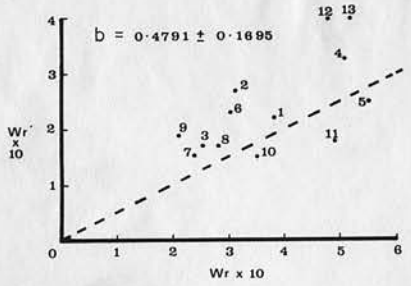


Figure 4-5. Wr, Vr graph, F1 1970.

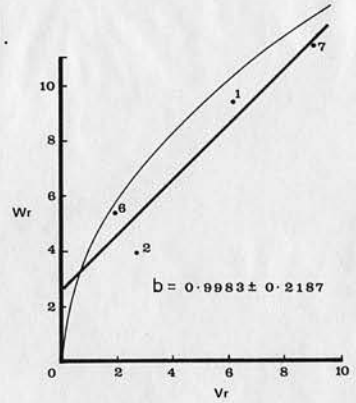
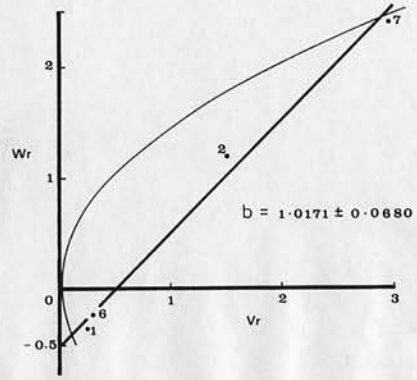


Figure 4-6. Wr, Vr graph, block 1, F1 1971.



Figures 4-5 and 4-6 6-rowed genotypes.

PRODUCTIVE TILLER NUMBER

of those for arrays 13 and 8 whose displacements were almost entirely responsible for the regression.

Although clear evidence for the existence of non-additive effects could not be demonstrated when the values of Wr+Vr over arrays were tested with the differences over blocks, significant correlations between yr, the parent mean, and Wr+Vr were obtained in the data from the 2-rowed population in 1970 and from the 6-rowed population in 1971. These correlations were negative suggesting that dominance was acting towards greater numbers of tillers.

Taken with the results of the analyses of variance (tables 4-2 and 4-3), the evidence from the W/V analyses points towards the existence of some non-additive gene action which, however, may be obscured by environmental effects, in the inheritance of this character though determination was predominatly additive.

The analysis for epistasis described by Hayman (1957) was performed on the 13 x 13 half diallels in both seasons. Chi-squared values for epistasis were significant with the exception of that for block 2 in 1971. In the 1970 data three of the epistatic crosses produced more tillers than their respective better parents in block 1 and four in block 2 (table 4-6a). These crosses involved parents 8, 12 and 13 in both blocks. In the 1971 data five epistatic crosses showed heterosis in block 1 and three in block 2. Parents 6, 8 and 12 were involved in these crosses in both blocks

TABLE 4-6

Mean tiller number for hybrids showing heterosis

a) 13 x 13 half diallel, 1970

	Block I			Block II		
	number of heterotic crosses	hybrid mean F_1	F_2	number of heterotic crosses	hybrid mean F_1	F_2
epistasis	3*	3.83	2.09	4*	3.88	3.38
mean of better parents		3.37			3.20	
no epistasis	16	3.99	3.52	16	3.45	3.09
mean of better parents		3.63			2.98	

* two complementary, one duplicate.

* two complementary, two duplicate.

b) 13 x 13 half diallel, 1971

epistasis	5*	5.54	3.00	3*	4.83	2.97
mean of better parents		4.38			4.00	
no epistasis	39	4.44	3.57	51	4.62	4.00
mean of better parents		3.90			3.87	

* all epistatic crosses complementary.

(table 4-6b).

For the estimation of the seven components of variation, twelve statistics were available from the pooled F_1 and F_2 data. An unweighted least squares analysis was performed (Mather, 1949; Mather and Vines, 1952; Mather and Jinks, 1971) and the components for the 13 x 13 half diallels are given with their standard errors in table 4-7. The estimate of D, the additive component, was highly significant in all cases as were the environmental components. However, the estimates for H_1, H_2 and F were generally not significant. Ratios of the various components are shown but are not meaningful where a component or components involved in their calculation failed to reach significance. The values for the seven components were used to reconstruct expected values for the statistics and the overall deviation of observed from expected was tested against heterogeneity between blocks (Mather and Jinks, 1971). The deviation item was not significant. At the level of accuracy obtained in this experiment therefore, the model could not be shown to be inappropriate.

Analysis of variance to test the fit to the additive-dominance model of the estimated components of variation for the 13 x 13 diallel set, 1970

Item	df	MS	F
Overall deviation	5	0.00188	2.81 N.S.
Heterogeneity	5	0.00067	
Total	10		

TABLE 4-7

Components of variation for tiller number in two seasons, 13 x 13 diallel, data for F_1 and F_2 pooled

	1970		1971	
	Blocks		Blocks	
Component	I	II	I	II
D	0.733 ± 0.057	0.496 ± 0.042	0.527 ± 0.096	0.308 ± 0.075
H_1	0.304 ± 0.230	0.613 ± 0.171	0.355 ± 0.386	0.685 ± 0.302
H_2	0.196 ± 0.225	0.369 ± 0.167	0.177 ± 0.378	0.449 ± 0.296
F	0.069 ± 0.154	0.198 ± 0.115	- 0.092 ± 0.259	-0.068 ± 0.203
E_o	0.145 ± 0.040	0.136 ± 0.030	0.242 ± 0.068	0.222 ± 0.053
E_1	0.193 ± 0.037	0.179 ± 0.028	0.305 ± 0.063	0.267 ± 0.049
E_2	0.244 ± 0.031	0.228 ± 0.023	0.315 ± 0.051	0.218 ± 0.040
$(H_1/D)^{\frac{1}{2}}$	0.644	1.110	0.820	1.491
$H_2/4H_1$	0.162	0.151	0.125	0.164
$\frac{1}{2}F/\sqrt{[D(H_1-H_2)]}$	0.123	0.285	- 0.150	- 0.126
$(4DH_1)^{\frac{1}{2}} + F/(4DH_1)^{\frac{1}{2}} - F$	1.158	1.438	0.807	0.862

Table 4-8 shows the components of variation estimated for the 9 x 9 half diallel comprising 2-rowed genotypes only. Ratios were not computed where the components did not approach significance. The additive component, D was small and mostly insignificant, indicating only small phenotypic differences between the parents, and the components H_1 and H_2 also failed to reach significance except in block II in 1971. When the overall deviation of observed from expected was tested against heterogeneity between blocks, significant deviation was found for the 1970 data but not for that of 1971. A significant deviation item indicates a failure of the model.

In order to test the relative magnitudes of D and H_1 as estimated in the various parts of the experiment, the mean values, $\bar{W}r$ and $\bar{V}r$, were corrected for their environmental components. Thus at F_1,

$$\bar{W}r = \tfrac{1}{2}D - \tfrac{1}{4}F + \frac{1}{n}E_o$$

and

$$\bar{V}r = \tfrac{1}{4}D - \tfrac{1}{4}F + \tfrac{1}{4}H_1 + \frac{1}{n}E_o + \frac{n-1}{n}E_1$$

where E_o and E_1 are the environmental variances for parents and hybrids respectively, and n is the number of parental lines. After subtracting the environmental terms,

$$\bar{W}r - \bar{V}r = \tfrac{1}{4}D - \tfrac{1}{4}H_1 .$$

Considering the 13 x 13 half diallels at F_1 in both seasons, $\bar{W}r-\bar{V}r$ was found to be 0.0743 ± 0.0293 for 1970 and -0.0149 ± 0.0292 in 1971. The standard errors were

TABLE 4-8

Components of variation for tiller number in two seasons, 9 x 9 diallel of 2-rowed genotypes, data for F_1 and F_2 pooled

Component	1970 Blocks I	1970 Blocks II	1971 Blocks I	1971 Blocks II
D	0.3243 ± 0.050	0.0850 ± 0.068	0.1307 ± 0.111	0.0085 ± 0.065
H_1	0.3665 ± 0.201	0.5202 ± 0.275	0.7076 ± 0.446	0.9803 ± 0.261
H_2	0.3055 ± 0.196	0.3416 ± 0.269	0.5590 ± 0.437	0.9623 ± 0.255
F	0.3171 ± 0.134	0.1141 ± 0.184	-0.0132 ± 0.299	-0.0443 ± 0.175
E_o	0.1632 ± 0.035	0.1678 ± 0.048	0.3027 ± 0.078	0.2568 ± 0.046
E_1	0.2402 ± 0.032	0.1981 ± 0.044	0.3464 ± 0.072	0.3592 ± 0.042
E_2	0.2852 ± 0.027	0.2599 ± 0.036	0.4099 ± 0.059	0.2472 ± 0.035
$(H_1/D)^{\frac{1}{2}}$	1.063	-	-	-
$H_2/4H_1$	0.208	-	-	0.245
$\frac{1}{2}F/\sqrt{\left[D(H_1-H_2)\right]}$	1.127	-	-	-
$(4DH_1)^{\frac{1}{2}} + F/(4DH_1)^{\frac{1}{2}} - F$	2.703	-	-	-

obtained from the blocks x (Wr-Vr) mean square in the analysis of variance of (Wr-Vr) values (Mather and Jinks, 1971). Thus, whilst in the first season $\bar{W}r$ was found to be significantly larger than $\bar{V}r$, showing that $D > H_1$, in the second season $\bar{W}r$ and $\bar{V}r$ were of equal magnitude and thus D was equal to H_1.

Results of the analysis of the diallel between 2-rowed genotypes only, gave $\bar{W}r-\bar{V}r = -0.0149 \pm 0.0474$ and $\bar{W}r-\bar{V}r = -0.2240 \pm 0.0528$ for the first and second seasons respectively, showing that the dominance level was generally higher in proportion to D in this population and confirming results in table 4-8.

Using the analysis of Method 4, Model I (Griffing, 1956) significant items were found for general combining ability (g.c.a.) and in some cases for specific combining ability (s.c.a.). The analyses of variance are given in table 4-9. In order to obtain unbiased estimates, the parents were not included in the combining ability analysis. Estimates for g.c.a. and s.c.a. for the 13 x 13 diallels at F_1 are given in tables 4-10a and 4-10b. General combining ability effects were extremely consistent and the correlation coefficient between estimates for the two blocks in the two seasons were, $r = 0.8053$ ($P < 0.001$) and $r = 0.8560$ ($P < 0.001$). The correlation coefficient for the mean estimates for the two seasons was $r = 0.9340$ ($P < 0.001$). The 6-rowed genotypes showed large negative g.c.a. effects and the largest positive effects were shown by Sultan and Mosane.

TABLE 4-9

Combining ability analyses for tiller number, 13 x 13 half diallel, F_1

		1970		1971	
		Blocks		Blocks	
		I	II	I	II
Item	D.F.	M.S.	M.S.	M.S.	M.S.
General combining ability	12	2.462 ***	1.965 ***	2.883 ***	2.168 ***
Specific combining ability	65	0.249 *	0.244	0.351	0.364 *
Error		0.185(699d.f.)	0.186(694d.f.)	0.268(700d.f.)	0.243(701d.f.)

TABLE 4-10 a

Estimates of general ($\hat{g}_i$) and specific ($\hat{s}_{ij}$) combining ability effects for number of tillers, season 1970

	$\hat{s}_{ij}$											$\hat{g}_i$	
	2	3	4	5	6	7	8	9	10	11	12	13	I	II
1	0.2096	0.0823	-0.0267	0.0460	0.3005	-0.1849	0.7796	0.3460	-0.2086	-0.5995	-0.2631	-0.4813	-0.6969	-0.3614
	-0.3173	-0.1446	0.2372	-0.8537	0.3099	0.5999	0.7008	-0.0446	0.5190	-0.8628	0.0281	-0.1719		
2		-0.0813	0.5096	-0.5177	-0.0631	0.0514	-0.2840	0.5823	0.5278	0.0369	-0.6267	-0.3449	-0.7332	-0.2550
		0.0490	-0.2692	-0.8601	0.3036	0.5636	-0.3055	-0.6510	1.0127	0.6308	-0.2783	0.1217		
3			1.3023	-0.1249	-0.3704	0.2442	0.4087	-0.0249	-0.5795	0.1296	-0.3340	-0.6522	0.2741	0.3722
			-0.0964	0.1127	-0.0237	-0.4637	-0.5328	-0.4783	0.1854	-0.1964	0.7945	0.7945		
4				-0.1340	0.2205	-0.0649	0.1996	0.2660	-0.5886	-0.3795	-1.1431	-0.1613	0.2831	0.0904
				0.3945	0.5581	0.1181	0.6490	-0.3964	0.2672	-0.1146	-0.6237	-0.7237		
5					0.2933	0.4078	0.3723	0.3387	-0.2158	-0.3067	-0.3704	0.2114	0.2104	0.2813
					-0.3328	0.2272	0.6581	0.2127	-0.1237	0.0945	0.4854	-0.0146		
6						0.2623	-0.1731	-0.3067	0.0387	0.1478	0.4842	-0.8340	-0.2441	-0.4823
						0.3908	-0.1783	0.1763	-0.1601	-0.2419	-0.0510	-0.7510		
7							-1.2286	0.1078	-0.2467	0.0623	-0.1013	0.6805	-0.7587	-0.8423
							-1.1183	-0.0637	-0.6001	0.4181	-0.1910	0.1090		
8								-0.2277	-0.4822	-0.1731	0.9633	-0.1549	-0.0232	0.0268
								0.0672	0.2308	0.0490	-0.0601	-0.1601		

TABLE 4-10 a Cont'd.

Estimates of general ($\hat{g}_i$) and specific ($\hat{s}_{ij}$) combining ability effects for number of tillers, season 1970

							$\hat{s}_{ij}$					$\hat{g}_i$	
	2	3	4	5	6	7	8	9	10	11	12	13	I	II
9									-0.2158 -0.5146	-0.2067 0.2036	-0.2704 0.4945	-0.3886 0.9945	0.3104	-0.1278
10		Population mean, Block I =								0.4387 -0.0328	0.6751 -0.5419	0.8569 -0.2419	0.4650	0.0086
		3.3404 ± 0.048												
11		S.E. ($\hat{s}_{ij}$) = ± 0.387									0.2842 -0.0237	0.5660 0.0763	0.3559	0.2904
12		Population mean, Block II =										0.7023 -0.0328	0.6195	0.7995
		2.9338 ± 0.048												
13		S.E. ($\hat{s}_{ij}$) = ± 0.389											-0.0623	0.1995
												S.E. ($\hat{g}_i$-$\hat{g}_j$)	± 0.181	± 0.181

TABLE 4-10 b

Estimates of general ($\hat{g}_i$) and specific ($\hat{s}_{ij}$) combining ability effects for number of tillers, season 1971

	$\hat{s}_{ij}$												$\hat{g}_i$	
	2	3	4	5	6	7	8	9	10	11	12	13	I	II
1	0.0625	0.0716	0.4444	-0.1011	-0.2666	0.5234	0.3989	-0.2375	-0.0556	-0.1920	0.1807	-0.8284	-0.5416	-0.6349
	0.9750	-0.0750	-0.4387	-0.7659	-0.2841	-0.3241	0.4068	0.2977	0.4704	-0.0569	0.3704	-0.5750		
2		-0.3193	0.2534	-0.0920	0.2425	0.2325	0.0080	-0.0284	0.3534	0.9171	-0.7102	-0.9193	-0.7507	-0.6303
		-0.0796	-0.3432	0.1295	-0.1887	-0.5887	-0.5978	0.7931	0.0659	-0.1614	0.0659	-0.0796		
3			0.4625	-1.0829	0.0516	0.4416	0.5171	-0.5193	1.1625	-0.3738	-0.3011	-0.1102	0.2402	0.4197
			0.2068	-0.7205	0.2613	0.2213	-0.3478	0.1431	2.1159	-0.3114	-0.4841	-0.9296		
4				1.4898	-0.9756	-0.3856	0.3898	-1.0466	-0.7647	0.2989	-0.4284	0.2625	0.4675	0.4833
				0.1159	-0.3023	-0.6423	0.5886	0.1795	0.9522	-0.4750	-0.7478	0.9068		
5					-0.0211	0.1689	-0.4556	0.0080	-0.3102	-0.4466	0.6262	0.2171	0.4129	0.0106
					0.2704	0.3304	0.0613	-0.3478	-0.2750	-0.3023	0.3250	1.1795		
6						0.1234	0.2789	-0.0575	0.0244	0.0880	0.5607	-0.0484	-0.2216	-0.3713
						0.0122	0.1431	0.1341	-0.5932	0.2795	0.2068	0.0613		
7							0.2689	0.4325	-0.1856	-0.7220	-0.8493	-0.0584	-0.9116	-0.7313
							0.2031	0.0941	0.0668	0.8395	-0.4332	0.2213		
8								-0.1920	-0.0102	-0.3466	-0.8738	0.0171	-0.0871	0.0378
								0.1250	0.1977	0.1704	-0.3023	-0.6478		

TABLE 4-10 b Cont'd.

Estimates of general ($\hat{g}_i$) and specific ($\hat{s}_{ij}$) combining ability effects for number of tillers, season 1971

								$\hat{s}_{ij}$				$\hat{g}_i$	
2	3	4	5	6	7	8	9	10	11	12	13	I	II
9								0.4534	-0.2829	1.0898	0.3807	-0.0507	0.3469
								-0.7114	-0.4387	0.6886	-0.9569		
10	Population mean, Block I								-1.1011	-0.1284	0.5625	0.0675	0.1742
	= 4.2298 ± 0.058								-0.8659	-1.0387	-0.3841		
11	S.E. ($\hat{s}_{ij}$) = ± 0.469									1.2353	0.9262	0.9038	0.3015
										0.7341	0.5886		
12	Population mean, Block II										-0.4011	0.3311	0.4742
	= 4.3903 ± 0.056										0.6159		
13	S.E. ($\hat{s}_{ij}$) = ± 0.448											0.1402	0.1197
											S.E. ($\hat{g}_i$-$\hat{g}_j$)	± 0.219	± 0.209

The general combining ability of Golden Promise for this character was practically zero.

Specific combining ability effects were inconsistent between blocks and seasons. The correlation coefficients between the estimates for the two blocks in each season were $r = 0.1388$ ($P > 0.1$) and $r = 0.3090$ ($0.01 > P > 0.001$). The seasonal inconsistency confirmed the interactions between years and non-additive genetic variance detected earlier (tables 4-4 and 4-5).

Number of grains per ear

The mean number of grains per ear in each season for the thirteen parental varieties are shown in table 4-11.

Considerable heterogeneity of the within-family variances was detected in both seasons. The highest variances were associated with the 6-rowed parents and their crosses and when the 2-rowed and the 6-rowed populations were analysed separately the heterogeneity was found to be much reduced. Thus the high level of heterogeneity in the population as a whole was found to be largely a result of inherently different levels of variance associated with two sub-groups. This was not entirely the case, however, as heterogeneity of variances was detected in the sub-population consisting only of 2-rowed by 6-rowed hybrids.

All analyses were conducted on untransformed data but the apparently non-random occurrence of widely

TABLE 4-11

Number of grains per ear (means of 10 plants) for 13 parent varieties in each of 2 replicate blocks for 2 seasons

		1970			1971		
		I	II	Mean	I	II	Mean
1.	Olli *	26.33	26.22	26.28	44.20	33.10	38.65
2.	Pirkka *	29.90	33.40	31.65	47.22	38.56	42.89
3.	Cambrinus	17.22	15.20	16.21	20.44	19.20	19.82
4.	Ymer	16.30	16.10	16.20	20.50	19.40	19.95
5.	Deba Abed	18.50	19.50	19.00	22.50	24.10	23.30
6.	Scotch Bere *	26.10	28.70	27.40	40.20	42.50	41.35
7.	O.A.C. 21 *	24.37	31.57	27.97	38.50	40.43	39.47
8.	Golden Promise	17.00	16.67	16.84	21.50	20.30	20.90
9.	Maris Baldric	16.40	19.00	17.70	21.40	19.00	20.20
10.	Midas	20.10	20.10	20.10	22.00	23.70	22.85
11.	Mosane	15.22	17.00	16.11	21.00	18.40	19.70
12.	Sultan	13.60	15.11	14.36	21.30	17.80	19.55
13.	Boreham Warrior	18.00	16.20	17.10	23.40	21.33	22.37
			$\pm$1.61	$\pm$1.14		$\pm$2.01	$\pm$1.42
	Mean	19.93	21.14		28.01	25.99	
			$\pm$0.45			$\pm$0.56	

* indicates 6-rowed parents

TABLE 4-12

Analyses of variance for number of grains per ear for full diallels in each of 2 seasons

Item	D.F.	9 x 9 F_1 1970 M.S.	9 x 9 F_1 1971 M.S.
a	8	1248.00 ***	3320.56 ***
b_1	1	302.04 ***	1001.83 ***
b_2	8	40.47	223.84 ***
b_3	27	351.34 ***	454.38 ***
b	36	280.89 ***	418.36 ***
c	8	84.52 ***	56.02 ***
d	28	52.50 ***	90.68 ***
Blocks	1	34.36	1700.37 ***
Ba	8	48.08 *	116.07 **
Bb_1	1	11.22	5.65
Bb_2	8	22.83	125.63 **
Bb_3	27	27.60	36.64
Bb	36	26.09	55.56
Bc	8	10.40	11.70
Bd	28	16.86	56.53
Bt	80	23.49	57.56 *
Within-family variance		22.02 (610 d.f.)	43.46 (628 d.f.)

All effects tested against the within-family variance

TABLE 4-13

Analyses of variance for number of grains per ear for half diallels in each of 2 seasons for F_1 and F_2

Item	D.F.	13 x 13 F_1 1970 M.S.	13 x 13 F_1 1971 M.S.	13 x 13 F_2 1970 M.S.	13 x 13 F_2 1971 M.S.
a	12	939.81 ***	3606.75 ***	1923.01 ***	5046.39 ***
b_1	1	386.61 ***	1807.60 ***	1.35	100.41
b_2	12	135.76 ***	632.59 ***	55.22 ***	223.65 ***
b_3	65	217.81 ***	271.11 ***	114.59 ***	130.12 ***
b	78	207.35 ***	346.42 ***	104.00 ***	144.13 ***
Blocks	1	0.01	2090.52 ***	0.43	1558.02 ***
Ba	12	40.90 **	90.75 **	36.85 *	166.98 ***
Bb_1	1	109.90 *	1.03	105.27 *	2.36
Bb_2	12	35.15 *	50.68	32.67 *	68.74 *
Bb_3	65	20.16	29.97	48.27 ***	107.19 ***
Bb	78	23.62	32.79	46.60 ***	99.93 ***
Bt	90	25.92 **	40.51	45.30 ***	108.87 ***
Within-family variance (F_1 and parents)		17.19 (1566 d.f.)	34.21 (1608 d.f.)		

All effects tested against the within-family variance

TABLE 4-14

Analysis of variance for number of grains per ear for half diallels in each of 2 seasons for 2-rowed genotypes at F_1 and F_2

Item	D.F.	2-rowed F_1 1970 M.S.	2-rowed F_1 1971 M.S.	2-rowed F_2 1970 M.S.	2-rowed F_2 1971 M.S.
a	8	9.86 ***	12.10 ***	10.54 ***	7.63 ***
b_1	1	43.67 ***	33.60 ***	18.36 **	26.00 ***
b_2	8	0.60	1.18	1.66	1.89
b_3	27	1.41	1.99 *	2.57	1.11
b	36	2.41	2.69 **	2.81	1.98
Blocks	1	3.29	29.19 ***	4.67	11.33 *
Ba	8	0.85	0.55	0.87	0.50
Bb_1	1	2.48	0.02	3.06	1.36
Bb_2	8	1.38	1.87	1.14	2.01
Bb_3	27	1.90	1.00	2.24	1.82
Bb	36	1.80	1.16	2.02	1.84
Bt	44	1.59	1.03	1.77	1.57

All effects tested against Bt

differing variances will be discussed later.

The analyses of variance (Hayman, 1954b) are shown in tables 4-12 and 4-13 for the full and half diallel sets respectively. Highly significant additive and non-additive effects were indicated in all the analyses and evidence of reciprocal effects was detected in the full diallel sets in both seasons. Analyses for the population comprising 2-rowed genotypes only are shown in table 4-14 from which it will be noted that the non-additive component of the variance was contained almost entirely in the $\underline{b}_1$ item.

Regressions of Wr on Vr for the full diallel and the half diallel sets at F_1 gave coefficients close to unity with the points representing arrays of 6-rowed parents forming a cluster with high values of Vr and Wr, far removed from the cluster representing arrays of 2-rowed parents which was close to the origin. By plotting standardized values of $\underline{y}_r$, the parental mean, against W_r+V_r, an inverse measure of dominance, it was clearly demonstrated that dominance was acting in the direction of low numbers of grains per ear, corresponding to 2-rowed vs 6-rowed expression (figure 4-7).

After correcting $\bar{W}r-\bar{V}r$ for their environmental components, $\bar{W}r-\bar{V}r$ was found to be -2.812 ± 0.549 and 2.435 ± 1.003 for the 1970 and 1971 data respectively (Mather and Jinks, 1971). Over-dominance was therefore apparent in the 1970 data whereas in 1971 dominance was incomplete.

Figure 4–7. Standardized deviations for yr and Wr+Vr, F_1 1970.

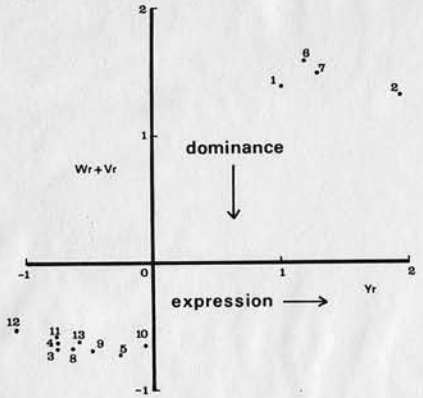


Figure 4–8. Wr, Vr graph, F_2 1970.

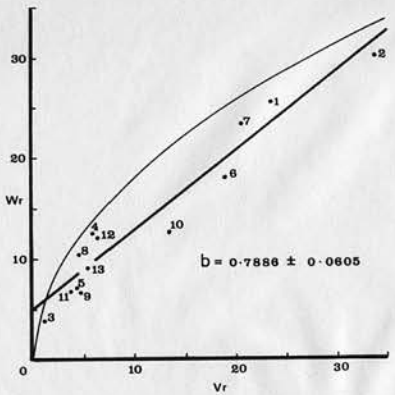


Figure 4–9. Wr, Vr graph, F_2 1971.

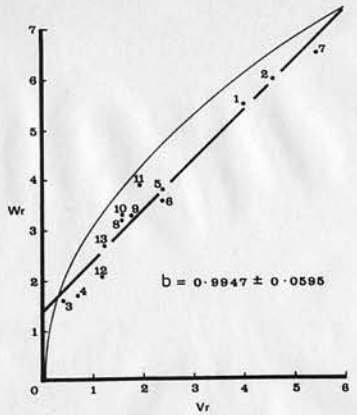


Figure 4–10. Standardized deviations for yr and Wr+Vr, block 1 F_1 1970.

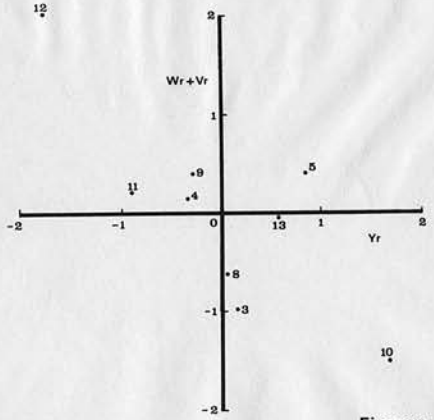
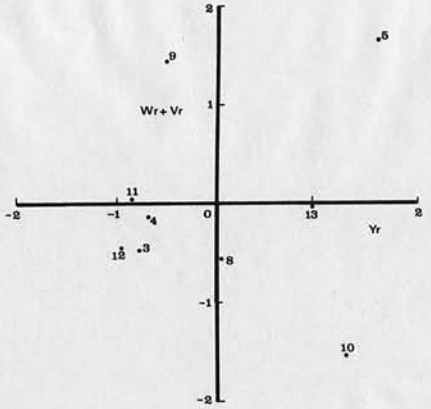


Figure 4–11. Standardized deviations for yr and Wr+Vr, F_1 1971.



Figures 4–10 and 4–11 2–rowed genotypes.

GRAINS PER EAR

At F_2, with dominance halved, the regressions were more easily plotted and the graphs for the half diallel in each season are shown in figures 4-8 and 4-9. The graphs are for means over blocks since the regression coefficients for each block did not differ significantly.

The analysis of variance of the estimates of (Wr+Vr) and (Wr-Vr) for the 13 x 13 F_1 diallel set, 1970

Item	df	MS	F
(Wr+Vr) Array differences	12	2415.18	9.24 ***
(Wr+Vr) Block differences	13	261.31	
(Wr-Vr) Array differences	12	8.80	1.12 N.S.
(Wr-Vr) Block differences	13	7.84	

The extreme recessive positions for the arrays for 6-rowed parents were still evident and, of the 2-rowed arrays, the point for Cambrinus (3) occupied the extreme dominant position in both seasons. The correlations between $\underline{y}_r$ and Wr+Vr were high and positive ($r = 0.9320$, $P < 0.001$, and $r = 0.8249$, $P < 0.001$ for the 1970 and 1971 seasons respectively) confirming that dominance was acting in the direction of low expression of the character.

Considering 2-rowed genotypes only, W/V analyses were inconsistent. The data for block 1 in 1970 gave a regression coefficient close to unity whilst that in block 2 was not significantly different from zero. The 1971 data gave non-significant regression coefficients for

both replicate blocks.

The analysis of variance of the estimates of (Wr+Vr) and (Wr-Vr) for the 13 x 13 F_1 diallel set, 1971

Item	df	MS	F
(Wr+Vr) Array differences	12	8524.36	16.42 ***
(Wr+Vr) Block differences	13	519.11	
(Wr-Vr) Array differences	12	65.66	2.51 N.S.
(Wr-Vr) Block differences	13	26.16	

After correcting $\bar{W}r$ and $\bar{V}r$ for their environmental components, D was shown to be equal to H_1 by $\bar{V}r/\bar{W}r \doteq 1$ (Jinks, 1954) except for block 1 in 1971, and it will be shown later (table 4-17) that gene frequencies were approximately equal, at least in the 1970 experiment, over all loci. The failure of the W/V test for the 2-rowed genotypes at F_1 must therefore be attributed to gene interaction. At F_2 regressions of Wr on Vr again showed departures from a slope of 1.

The relationship between parental expression and degree of dominance for the F_1 generation was best shown by plotting standardized values for $\underline{y}_r$ and Wr+Vr (figures 4-10 and 4-11). The graphs for the two seasons were similar particularly with respect to arrays 5, 8, 10 and 13.

Correlations between $\underline{y}_r$ and Wr+Vr for F_2 data were negative in both seasons ($r = -0.8034$, $P < 0.01$, and

$r = -0.6792$, $P < 0.05$ respectively). Within the 2-rowed genotypes dominance was thus found to be acting in the direction of greater numbers of grains.

The analysis for epistasis described by Hayman (1957) was performed on the 9 x 9 half diallels involving only 2-rowed parents. Chi-squared values for epistasis were not significant, with the exception of that for one replicate block in the 1970 season ($P < 0.05$). When the C-scaling test was performed on the 13 x 13 half diallels, significant interactions were detected but no one array showed conspicuously more interacting crosses than any of the others and interactions were not generally consistent between blocks. Of the interacting crosses most were of the duplicate type though in general the degree of epistasis detected was slight.

Tables 4-15a and 4-15b show mean values for hybrids exhibiting heterosis, that is higher expression of the character than that of either parent, in the 9 x 9 diallels of 2-rowed parents. In the first season 67% of the hybrids showed heterosis which averaged 10% in F_1 over the mean of the better parents. In the second season 68% of hybrids were heterotic giving an average increase at F_1 of 6% over the mean of the better parents. Taking the total 36 crosses for each diallel and comparing each with the parent giving the higher expression of the character showed an average increase of 4.0% in 1970, the poorer of the two seasons, and 1.6% in 1971.

For the estimation of the seven components of

TABLE 4-15

Mean number of grains per ear for hybrids showing heterosis

a) 9 x 9 half diallel of 2-rowed genotypes, 1970

	Block I			Block II		
	number of heterotic crosses	hybrid mean F_1	hybrid mean F_2	number of heterotic crosses	hybrid mean F_1	hybrid mean F_2
epistasis	2*	19.70	18.26	2*	20.86	21.65
mean of better parents		17.00			19.80	
no epistasis	27	18.59	18.42	17	19.10	17.67
mean of better parents		17.92			17.36	

* one complementary, one duplicate.

* one complementary, one duplicate.

b) 9 x 9 half diallel of 2-rowed genotypes, 1971

epistasis	2*	21.95	24.87	1*	22.60	24.90
mean of better parents		21.50			21.33	
no epistasis	26	23.60	22.43	20	22.25	20.81
mean of better parents		22.07			20.49	

* all epistatic crosses of the duplicate type

variation, twelve statistics from the pooled F_1 and F_2 data were used. The components with their standard errors are given in tables 4-16 and 4-17.

Considering the results from the 13-parent diallel sets in 1970 and 1971 (table 4-16), the existence of high dominance indicated by the graphical analysis was confirmed by $(H_1/D)^{\frac{1}{2}} \doteq 1$. The values of H_1 and H_2 in the 1970 experiment were very similar, indicating equal gene frequencies, but the 1971 results showed H_1 as somewhat larger than H_2. In addition the large positive values of F further suggest inequality of gene frequencies with an excess of dominant over recessive alleles. The ratio of $\underline{h}$ to $\underline{d}$ as measured by the quantity $\frac{1}{2}F\Big/\sqrt{D\left[(H_1-H_2)\right]}$ in 1971 was apparently constant.

Very similar conclusions could be drawn from table 4-17 which shows the components estimated for the population of 2-rowed genotypes. In the absence of the 2-rowed vs 6-rowed comparison, which might have accounted for all the dominance measured in the 13-parent diallel set, considerable dominance was again demonstrated, confirming results in table 4-14 and figures 4-10 and 4-11. Again, approximately equal gene frequencies were indicated by $H_2/4H_1 \doteq 0.25$ in the 1970 experiment. The data for block 1 in 1971 gave markedly atypical values for the components and the ratios were not calculated.

The values for the seven components were used to reconstruct values for the statistics and the overall deviation of observed from expected was tested against

TABLE 4-16

Components of variation for grains per ear in two seasons, 13 x 13 half diallel, F_1 and F_2 data pooled

Component	1970 Blocks I	1970 Blocks II	1971 Blocks I	1971 Blocks II
D	24.79 ± 2.40	40.96 ± 2.75	101.58 ± 5.52	80.69 ± 4.09
H_1	21.22 ± 9.67	41.48 ± 11.07	54.92 ± 22.26	58.18 ± 16.48
H_2	23.59 ± 9.46	43.20 ± 10.84	46.21 ± 21.79	47.69 ± 16.13
F	14.76 ± 6.48	26.01 ± 7.43	60.83 ± 14.93	51.39 ± 11.05
E_o	1.96 ± 1.70	1.56 ± 1.95	4.28 ± 3.91	3.98 ± 2.90
E_1	1.87 ± 1.57	2.49 ± 1.80	4.75 ± 3.61	3.60 ± 2.67
E_2	4.19 ± 1.28	5.84 ± 1.49	9.56 ± 2.95	9.21 ± 2.18
$(H_1/D)^{\frac{1}{2}}$	0.92	1.01	0.73	0.85
$H_2/4H_1$	0.28	0.26	0.21	0.20
$\frac{1}{2}F/\sqrt{\left[D(H_1-H_2)\right]}$			1.02	0.88
$(4DH_1)^{\frac{1}{2}} + F/(4DH_1)^{\frac{1}{2}} - F$	1.95	1.92	2.37	2.20

TABLE 4-17

Components of variation for grains per ear in two seasons

2-rowed genotypes only, F_1 and F_2 data pooled

	1970		1971	
	Blocks		Blocks	
Component	I	II	I	II
D	2.49 ± 0.18	2.11 ± 0.39	- 0.47 ± 0.20	3.30 ± 0.41
H_1	2.26 ± 0.72	3.67 ± 1.55	0.30 ± 0.79	4.38 ± 1.67
H_2	2.23 ± 0.70	4.10 ± 1.52	0.39 ± 0.78	3.16 ± 1.63
F	1.55 ± 0.48	0.04 ± 1.04	- 2.36 ± 0.53	2.62 ± 1.12
E_o	1.06 ± 0.13	1.39 ± 0.27	1.39 ± 0.14	1.74 ± 0.29
E_1	1.04 ± 0.12	0.89 ± 0.25	1.35 ± 0.13	1.15 ± 0.27
E_2	1.13 ± 0.09	2.53 ± 0.21	1.65 ± 0.11	1.38 ± 0.22
$(H_1/D)^{\frac{1}{2}}$	0.95	1.32		1.15
$H_2/4H_1$	0.25	0.28		0.18
$(4DH_1)^{\frac{1}{2}} + F/(4DH_1)^{\frac{1}{2}} - F$	1.97	1.01		2.05

heterogeneity between blocks (Mather and Jinks, 1971). In the case of the 13-parent diallel sets in 1970 and 1971 the overall deviation item was found to be significant. This indicates a failure of the model due to epistasis. The goodness of fit of the model was similarly tested for the components derived from the population composed of 2-rowed genotypes only and in this case the overall deviation was not significantly greater than the heterogeneity among the parts of the experiments. Such a result does not necessarily, however, indicate that the fit of the model is good, but merely that at the level of accuracy of the experiments the model cannot be shown to be inappropriate.

The mean data over replicate blocks for the 13 x 13 F_1 half diallels in each season were analysed using the Method 4, Model I analysis of Griffing (1956). The analysis of variance revealed significant variances associated with general combining ability and specific combining ability in both seasons and the combining ability effects are shown in table 4-18. Calculation of the correlation between effects estimated in the two seasons gave $r = 0.7089$, $P < 0.01$ for g.c.a. effects and $r = 0.7690$, $P < 0.001$ for s.c.a. effects. Most of the 2-rowed parents gave negative g.c.a. effects and, as expected, negative s.c.a. effects were detected for all crosses between 2-rowed and 6-rowed parents.

When data for the 2-rowed genotypes in each block were analysed in each season (tables 4-19 and 4-20)

TABLE 4-18

General ($\hat{g}_i$) and specific ($\hat{s}_{ij}$) combining ability effects for grains per ear, F_1 data

	$\hat{s}_{ij}$ 1970 and 1971 (below) estimates											$\hat{g}_i$	
	2	3	4	5	6	7	8	9	10	11	12	13	1970	1971
1	5.923	-2.885	-1.777	-3.612	9.283	7.628	-1.700	-1.567	-3.114	-2.832	-2.408	-2.939	1.234	1.926
	13.154	-2.930	-2.839	-2.936	5.245	9.070	-3.450	-4.613	1.394	-2.635	-4.243	-5.211		
2		-2.509	-2.602	-3.037	6.428	7.323	-2.585	-3.251	-2.448	0.093	-1.073	-2.274	2.059	2.419
		-4.073	-4.532	-3.560	5.141	12.447	-3.953	-2.347	-4.100	-2.439	-2.437	-3.304		
3			1.551	1.636	-3.360	-2.554	1.578	0.471	1.134	0.746	1.990	2.189	-1.364	-2.947
			2.084	1.937	-3.392	-2.487	1.623	0.609	1.467	1.628	1.529	2.012		
4				1.353	-2.582	-2.067	2.465	1.179	0.721	1.963	0.057	-0.264	-1.181	-1.188
				0.428	-0.052	-2.296	1.664	2.250	0.458	1.218	0.470	1.153		
5					-2.877	-3.681	1.721	1.944	2.517	0.119	1.532	2.391	-0.387	-1.591
					-4.299	-3.363	2.767	2.303	1.260	-0.269	2.273	3.456		
6						9.573	-3.165	-2.911	-1.329	-3.917	-1.863	-3.294	2.049	9.739
						0.358	-2.862	0.374	0.581	-0.958	-0.856	0.727		
7							-2.350	-3.246	-2.843	-3.721	-2.428	-1.649	2.253	-0.917
							-0.427	-2.941	-2.913	-3.082	-1.251	-3.118		

TABLE 4-18 Cont'd.

General ($\hat{g}_i$) and specific ($\hat{s}_{ij}$) combining ability effects for grains per ear, F_1 data

												$\hat{g}_i$	
	2	3	4	5	$\hat{s}_{ij}$ 6	1970 and 1971 (below) 7	8	9	10	11	12	13	1970	1971
8								1.056	-0.131	1.821	1.174	0.103	-0.899	-1.477
								1.489	-1.503	1.808	0.859	1.992		
9									1.392	1.354	1.248	2.327	-0.872	-1.213
									1.533	-0.026	1.696	-0.322		
10		1970 population mean ($\hat{u}$)								2.147	1.111	0.850	0.065	0.229
		= 19.21 $\pm$ 0.149								1.001	0.553	0.276		
11		S.E. ($\hat{s}_{ij}$) = $\pm$ 1.206									0.172	2.051	-0.997	-2.282
											1.414	2.347		
12		1971 $\hat{u}$ = 24.15 $\pm$ 0.209										0.495	-1.340	-2.133
		S.E. ($\hat{s}_{ij}$) = $\pm$ 1.687										-0.002		
13													-0.619	-0.566
											S.E. ($\hat{g}_i$-$\hat{g}_j$)		$\pm$0.563	$\pm$0.788

TABLE 4-19

General and specific combining ability effects for grains per ear, F_1 data, 1970, 2-rowed genotypes only

	$\hat{s}_{ij}$ Replicate blocks I and II (below)								$\hat{g}_i$	
	4	5	8	9	10	11	12	13	I	II
3	-0.4457	1.2428	-0.1814	-0.0386	-1.3457	0.7471	0.1000	-0.0786	-0.4067	-0.3343
	1.0450	-1.6764	0.6178	-2.0864	0.9007	-2.1507	1.7250	1.6250		
4		-1.2129	2.4628	-0.7943	0.4286	0.5914	-0.5557	-0.4743	-0.4510	-0.5757
		0.8650	0.3893	0.7350	-1.0579	1.0907	-0.8336	-2.2336		
5			0.6314	0.5743	-0.1329	-1.1400	-1.6572	1.6943	0.4805	1.2757
			-0.4622	-0.2964	1.9007	-2.0607	2.0150	-0.2850		
8				-0.7500	-0.7572	-0.4643	1.1886	-2.1300	-0.0952	-0.1486
				0.2278	-1.7850	1.6336	-0.5607	-0.0607		
9					0.6857	-0.3214	-0.1686	0.8128	0.0619	0.0857
					-0.5193	0.2293	0.6050	1.1050		
10	Replicate block I population mean ($\hat{u}$)					0.0714	1.0243	0.0257	1.2690	0.3986
	= 19.08 ± 0.167					1.7764	-0.5079	-0.7079		
11							0.2171	0.2986	-0.1238	-0.1500
	S.E. ($\hat{s}_{ij}$) = ± 0.868						-1.7593	1.2407		
12								-0.1486	-0.5767	-1.1257
	Replicate block II population mean ($\hat{u}$)							-0.6836		
13	= 18.53 ± 0.197								-0.1581	0.5743
	S.E. ($\hat{s}_{ij}$) = ± 1.026								S.E. ($\hat{g}_i - \hat{g}_j$) ± 0.536	± 0.633

TABLE 4-20

General and specific combining ability effects for grains per ear F_1 data, 1971, 2-rowed genotypes only

	$\hat{s}_{ij}$ Replicate blocks I and II (below)								$\hat{g}_i$	
	4	5	8	9	10	11	12	13	I	II
3	1.3057	-0.5228	0.0057	-2.3743	0.7629	-0.1457	0.7200	0.2486	-0.8130	-1.3575
	-0.3533	-0.0847	-0.2533	0.4325	0.2910	0.3582	-0.6104	0.2196		
4		-1.0943	0.5343	0.9543	0.0914	-0.9171	-0.2514	-0.6228	0.2584	0.1854
		-1.6275	0.2039	1.2896	-0.1518	1.2153	-0.8533	0.2767		
5			-0.1943	1.7257	-0.5371	-0.9457	0.2200	1.3486	0.6870	0.2168
			1.8725	-0.6418	0.8167	-2.9961	1.0153	1.6453		
8				1.2543	-1.8086	0.0829	-1.1514	1.2772	0.2584	-0.1146
				-0.8104	-2.4518	1.1153	0.5467	-0.2233		
9					1.1114	-1.1371	0.9686	-2.5028	-0.3616	0.6997
	Replicate block I population mean ($\hat{u}$)				1.0339	-0.9990	0.4325	-0.7375		
10	= 23.05 ± 0.186					1.0400	0.0057	-0.6657	1.0013	0.9411
	S.E. ($\hat{s}_{ij}$) = ± 0.968					0.1596	0.3910	-0.0890		
11							0.2972	1.7257	-0.9902	-0.9260
	Replicate block II population mean ($\hat{u}$)						0.6582	0.4882		
12	= 21.92 ± 0.183							-0.8086	-0.9559	-0.7575
	S.E. ($\hat{s}_{ij}$) = ± 0.955							-1.5804		
13									0.9156	1.1125
							S.E. ($\hat{g}_i - \hat{g}_j$)		± 0.598	± 0.589

TABLE 4-21

Analysis of variance for number of grains per ear for full diallels over two seasons

Item	D.F.	M.S.
a	8	807.07 ***
b_1	1	240.39 ***
b_2	8	35.92 ***
b_3	27	145.53 ***
c	8	14.21
d	28	18.98 ***
Total (between families)	80	144.48 ***
Years	1	2386.43 ***
Blocks (within years)	2	173.47 ***
Years x a	8	106.63 ***
Years x b_1	1	20.37
Years x b_2	8	16.94 *
Years x b_3	27	15.61 ***
Years x c	8	13.89
Years x d	28	9.66
Years x Total	80	22.65 ***
Block interactions	160	8.10

All effects tested against block interactions

TABLE 4-22

Analyses of variance for number of grains per ear for half diallels over two seasons at F_1 and F_2

Item	D.F.	13 x 13 F_1 M.S.	13 x 13 F_2 M.S.
a	12	383.63 ***	653.57 ***
b_1	1	193.29 ***	3.92
b_2	12	60.55 ***	22.88 ***
b_3	65	43.74 ***	14.84 ***
b	78	48.24 ***	15.94 ***
Total (between families)	90	92.96 ***	100.95 ***
Years	1	2418.77 ***	3088.34 ***
Blocks (within years)	2	104.53 ***	77.92 ***
Years x a	12	71.00 ***	43.36 ***
Years x b_1	1	26.13 **	6.26
Years x b_2	12	16.29 ***	5.01
Years x b_3	65	5.15 ***	9.63 ***
Years x Total	90	15.65 ***	13.47 ***
Block interactions	180	3.32	7.71

All effects tested against block interaction (F_1 + parents)

little consistency was apparent between seasons or between blocks for the s.c.a. effects. G.c.a. effects were more consistent however: Cambrinus (3), Mosane (11) and Sultan (12) exhibited negative effects in both seasons, whilst Midas (10) exhibited relatively high positive effects. With one exception significant positive correlations were detected between the g.c.a. effects and the corresponding 2-rowed parent expression of the character (table 4-11).

Analyses of variance (Hayman, 1954b) on data from both seasons (tables 4-21 and 4-22) showed, as expected, highly significant differences associated with years. In addition the analyses showed significant additive and non-additive effects x years interaction.

1000 Corn weight

The mean values for the thirteen parents are shown in table 4-23. The weights measured in the first season were very much lower than those obtained in 1971 and indeed, analyses of the data from 1970 gave less meaningful results than analyses of the data from 1971 as will be shown below. All analyses were conducted on untransformed data.

Analyses of variance (Hayman, 1954b) are given in tables 4-24 and 4-25 for the full and half diallel experiments respectively in each season. Tables 4-26 and 4-27 show the analyses over seasons. All the analyses revealed large additive and non-additive effects and the analysis of the full diallel in each season (table 4-24) showed significant d items indicating the

TABLE 4-23

1000 Corn weight (means of 10 plants) for 13 parent varieties in each of two blocks and two seasons

		1970			1971		
		I	II	Mean	I	II	Mean
1.	Olli *	27.56	28.04	27.80	38.93	37.48	38.21
2.	Pirkka *	26.34	28.12	27.23	37.77	35.69	36.73
3.	Cambrinus	34.43	30.35	32.39	47.92	42.72	45.32
4.	Ymer	27.83	27.63	27.73	42.43	43.75	43.09
5.	Deba Abed	25.08	27.26	26.17	42.76	43.55	43.16
6.	Scotch Bere *	28.67	29.40	29.04	39.53	40.70	40.12
7.	O.A.C. 21 *	28.15	32.41	30.28	37.13	34.77	35.95
8.	Golden Promise	23.10	25.62	24.36	35.05	33.81	34.43
9.	Maris Baldric	31.69	29.75	30.72	47.81	41.40	44.61
10.	Midas	25.75	27.63	26.69	37.12	33.89	35.51
11.	Mosane	27.22	28.42	27.82	43.27	40.62	41.95
12.	Sultan	26.87	26.19	26.53	43.53	40.70	42.12
13.	Boreham Warrior	31.06	34.10	32.58	52.29	48.65	50.47
			$\pm$1.247	$\pm$0.882		$\pm$1.970	$\pm$1.393
	Mean	27.98	28.84		41.96	39.83	
			$\pm$0.346			$\pm$0.546	

* indicates 6-rowed parents

TABLE 4-24

Analyses of variance for 1000 corn weight for the full diallel experiment in two seasons

Item	D.F.	9 x 9 F_1 1970 M.S.	9 x 9 F_1 1971 M.S.
a	8	290.61 ***	1260.94 ***
b_1	1	5206.93 ***	6479.42 ***
b_2	8	73.03 *	344.58 ***
b_3	27	752.60 ***	902.85 ***
b	36	725.31 ***	933.68 ***
c	8	37.68	17.26
d	28	46.76 *	70.22 **
Blocks	1	71.05	379.31 **
Ba	8	13.19	49.31
Bb_1	1	53.79	66.21
Bb_2	8	14.71	43.89
Bb_3	27	30.66	24.22
Bb	36	27.76	29.76
Bc	8	8.23	50.68
Bd	28	39.96	43.94
Bt	80	28.62	38.77
Within-family variance		30.07 (599)	40.19 (637)

TABLE 4-25

Analyses of variance for 1000 corn weight at F_1 and F_2 in two seasons

Item	D.F.	13 x 13 F_1 1970 M.S.	13 x 13 F_1 1971 M.S.	13 x 13 F_2 1970 M.S.	13 x 13 F_2 1971 M.S.
a	12	1177.58 ***	1653.11 ***	790.44 ***	1509.08 ***
b_1	1	10773.93 ***	16699.33 ***	2530.24 ***	3017.24 ***
b_2	12	327.98 ***	664.13 ***	180.75 ***	310.13 ***
b_3	65	479.48 ***	626.18 ***	184.19 ***	157.00 ***
b	78	588.15 ***	838.09 ***	213.74 ***	217.23 ***
Blocks	1	150.11 *	1215.69 ***	23.53	91.26
Ba	12	19.63	45.67	41.35	60.43
Bb_1	1	155.98 *	19.31	89.63	216.93 *
Bb_2	12	26.50	34.20	29.55	27.75
Bb_3	65	25.52	29.14	38.58 *	103.33 ***
Bb	78	27.34	29.80	37.84 *	93.16 ***
Bt	90	26.31	31.91	38.31 *	88.79 ***
Within-family variance (F_1 + Parents)		29.25 (1558 d.f.)	41.09 (1620 d.f.)		

TABLE 4-26

Analysis of variance for 1000 corn weight for the full diallel experiment over two seasons

Item	D.F.	M.S.
a	8	181.94 ***
b_1	1	2330.36 ***
b_2	8	55.88 ***
b_3	27	312.31 ***
b	36	311.38 ***
c	8	5.11
d	28	6.86
Total (between families)	80	161.23 ***
Years	1	13864.67 ***
Blocks (within years)	2	6.10
Years x a	8	128.38 ***
Years x b_1	1	6.94
Years x b_2	8	27.64 ***
Years x b_3	27	18.80 ***
Years x b	36	20.44 ***
Years x c	8	5.88
Years x d	28	16.53 ***
Years x Total	80	28.41
Block interactions	160	6.74

TABLE 4-27

Analyses of variance for 1000 corn weight in the half diallel experiment for F_1 and F_2 over two seasons

Item	D.F.	13 x 13 F_1 M.S.	13 x 13 F_2 M.S.
a	12	199.90 ***	150.59 ***
b_1	1	2714.89 ***	553.67 ***
b_2	12	81.67 ***	39.98 ***
b_3	65	102.45 ***	27.33 ***
b	78	132.75 ***	36.06 ***
Total (between families)	90	141.70 ***	51.33 ***
Years	1	17695.72 ***	14794.46 ***
Blocks (within years)	2	12.79 *	0.55
Years x a	12	83.17 ***	79.37 ***
Years x b_1	1	32.34 ***	1.07
Years x b_2	12	17.53 ***	9.11 ***
Years x b_3	65	8.12 ***	6.74 ***
Years x b	78	9.88 ***	7.03 ***
Years x Total	90	19.65 ***	16.68 ***
Block interactions	180	2.91	6.36
Grand Total	363		

All effects tested against block interaction M.S. for F_1 + parents

existence of reciprocal effects. Neither the c nor the d items reached significance, however, when the data from the two seasons were analysed together (table 4-26). Significant interactions were revealed between seasons and additive and non-additive genetic variance (tables 4-26 and 4-27).

Analysis of the data for 1970 showed non-significant coefficients for the regression of Wr on Vr. When array differences for the values of Wr-Vr and Wr+Vr were tested against their respective block interactions no significant differences were revealed. Since the existence of non-additive effects was indicated by the analyses of variance, it must be concluded that the present failure to detect either interaction or non-additive variance was due to large Wr-Vr x block and Wr+Vr x block interactions.

Regressions of Wr on Vr for the 1971 data gave coefficients significantly different from 1 in F_1 and F_2 (e.g. figure 4-12), and array differences between values of Wr-Vr and Wr+Vr were highly significant.

The analysis of variance of the estimates of (Wr+Vr) and (Wr-Vr) for the 13 x 13 F_1 diallel set, 1971

Item	df	MS	F
(Wr+Vr) Array differences	12	3317.97	73.97 ***
(Wr+Vr) Block differences	13	44.85	
(Wr-Vr) Array differences	12	642.03	23.52 ***
(Wr-Vr) Block differences	13	27.29	

Figure 4-12. Regression of Wr on Vr, F_1, 1971.

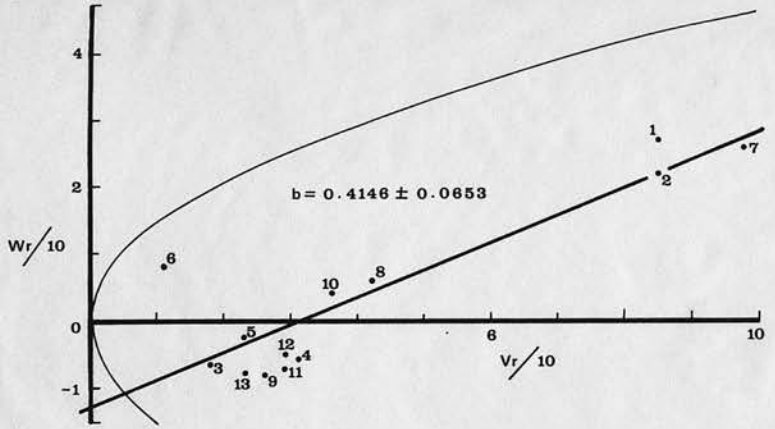


Figure 4-13. Regression of Wr on Vr, omitting the Scotch Bere array, F_1, 1971.

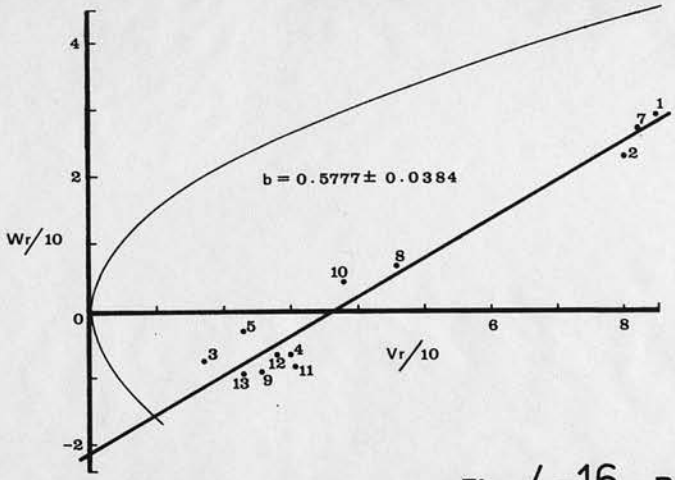


Fig. 4-14. Regression of Wr on Vr, F_1, 1971.

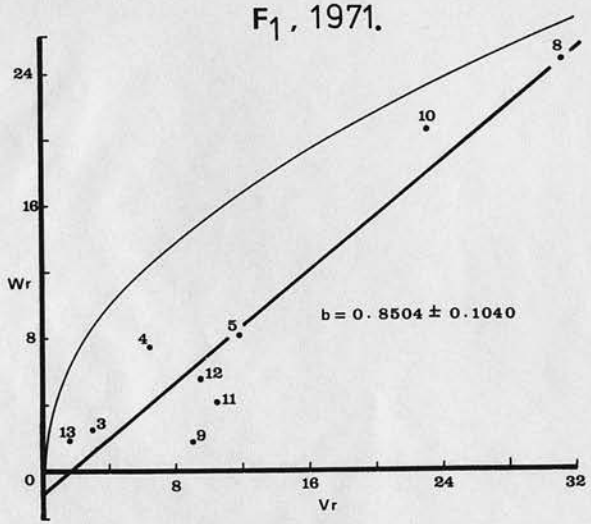


Fig. 4-15. Regression of Wr´ on Wr, F_1 1971.

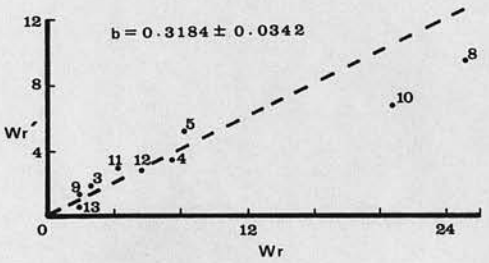
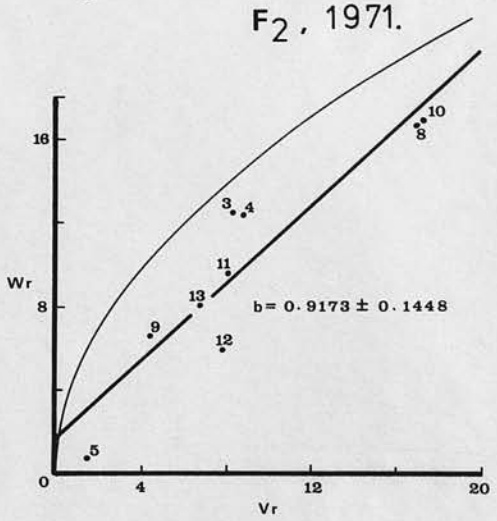


Fig. 4-16. Regression of Wr on Vr, F_2, 1971.



Figures 4-14 to 4-16 are for 2-rowed genotypes only.

1000 CORN WEIGHT

The array for Scotch Bere (6) showed conspicuous interaction and the regression analysis was performed omitting the data for this array (figure 4.13). Again, a slope departing markedly from unity was obtained and the intercept with the Wr axis indicated over-dominance. A marked separation of the arrays for 2-rowed genotypes and 6-rowed genotypes was observed with the points for 6-rowed genotypes at the extreme recessive end of the regression line.

When the mean values of Wr and Vr for each season were corrected for their environmental components the values for $\bar{W}r-\bar{V}r$ were -25.9835 ± 1.519 and -36.5736 ± 1.125 for the 1970 data and the 1971 data, with the Scotch Bere array omitted, respectively. This confirms the existence of over-dominance indicated by the graphs for the 1971 data.

Since the points for the 6-rowed genotypes appeared to be depressing the slope of the regression, the 1971 data for 2-rowed genotypes only were analysed and this revealed an absence of non-allelic interaction or correlated gene distribution. Regression coefficients close to unity were obtained in the F_1 and F_2 generations and, since the regression coefficients for each block were not significantly different, regressions were calculated for the mean values over blocks (figures 4-14, 4-15 and 4-16).

The analysis of variance of the estimates of (Wr+Vr) and (Wr-Vr) for the 9 x 9 F_1 diallel set of 2-rowed genotypes, 1971

Item	df	MS	F
(Wr+Vr) Array differences	8	623.541	21.05 ***
(Wr+Vr) Block differences	9	29.627	
(Wr-Vr) Array differences	8	16.624	< 1 N.S.
(Wr-Vr) Block differences	9	17.544	

Figures 4-14 and 4-16 show the extreme positions taken by the points representing the Golden Promise (8) and Midas (10) arrays at the recessive end of the regression line. These two points were entirely responsible for the depression of the slope for the regression of Wr' on Wr (figure 4-15) for the F_1 data. The positions of the two points below the line of slope $\frac{1}{2}$ indicates that they are unusual genotypes (Hayman 1958).

The value of $\bar{W}r-\bar{V}r$, after correcting $\bar{W}r$ and $\bar{V}r$ for environmental components, was found to be -1.426 ± 1.44. There was thus no significant difference between D and H_1 and dominance was complete. The correlation between $\underline{y}_r$ the parental mean, and Wr+Vr was - 0.8794, $P < 0.01$ showing that dominance was acting in the direction of increased expression of the character. This was also found to be the case for the 1971 data when all 6-rowed genotypes were included ($r = -0.6571$, $P < 0.05$) and when Scotch Bere only was omitted ($r = -0.7085$, $P < 0.01$) but no

correlation could be obtained for the 1970 data, confirming the low accuracy of these data.

Chi-squared values for epistasis (Hayman, 1957) were not significant for the 1970 data though eight individual crosses did exhibit epistasis. These were mostly of the duplicate type and with only two exceptions, were hybrids between 2-rowed and 6-rowed parents. All but one of the epistatic crosses exhibited heterosis (table 4-28a). Only one epistatic cross was common to both blocks.

In the analysis of the 1971 data a significant chi-squared value was obtained for block 1 only. A total of twelve individual crosses showed epistasis but none of these was common to both blocks. Of the twelve epistatic crosses ten were between 2-rowed and 6-rowed parents and all but one exhibited heterosis (table 4-28b).

A large proportion of the hybrids in the 13 x 13 half diallels showed higher expression than the better parent. The mean level of heterosis in the F_1 was +32% and +18% in the first and second seasons respectively. At F_2 the level had dropped to +20% and +2%. Clearly the 1971 figures are the more reliable.

Seven components were estimated using the twelve statistics available from the pooled F_1 and F_2 data. The over-dominance detected by the W/V analysis in the 13 x 13 half diallels was confirmed by the large values of H_1 and H_2 relative to D (table 4-29). The estimate of H_2 was somewhat lower than that of H_1 in both seasons indicating some inequality of gene frequencies. The low

TABLE 4-28

1000 Corn weight mean values for hybrids showing heterosis

a) 13 x 13 half diallel, 1970

	Block I			Block II		
	number of heterotic crosses	hybrid mean F_1	hybrid mean F_2	number of heterotic crosses	hybrid mean F_1	hybrid mean F_2
epistasis	3*	44.37	43.31	4*	39.39	35.13
mean of better parents		30.30			30.57	
no epistasis	62	36.15	31.95	60	36.03	32.12
mean of better parents		29.13			29.94	

* three duplicate

* two duplicate, two complementary.

b) 13 x 13 half diallel, 1971

epistasis	5*	50.39	38.66	6*	51.87	47.88
mean of better parents		44.16			41.43	
no epistasis	56	51.91	45.40	61	49.97	44.92
mean of better parents		44.26			42.43	

* five complementary

* four duplicate, two complementary.

TABLE 4-29

Components of variation for 1000 corn weight in two seasons

13 x 13 half diallel, data from F_1 and F_2 pooled

	1970		1971	
	Blocks		Blocks	
Component	I	II	I	II
D	7.573 ± 1.782	4.253 ± 1.360	22.726 ± 2.334	15.574 ± 2.019
H_1	130.765 ± 7.182	97.255 ± 5.481	145.680 ± 9.408	148.637 ± 8.137
H_2	112.967 ± 7.030	84.603 ± 5.365	117.293 ± 9.208	126.090 ± 7.964
F	4.621 ± 4.817	-2.811 ± 3.676	17.005 ± 6.309	16.986 ± 5.457
E_o	1.493 ± 1.263	1.499 ± 0.964	3.020 ± 1.654	4.507 ± 1.431
E_1	2.243 ± 1.165	2.543 ± 0.889	4.810 ± 1.526	4.979 ± 1.320
E_2	4.803 ± 0.951	5.338 ± 0.726	6.678 ± 1.246	8.226 ± 1.077
$(H_1/D)^{\frac{1}{2}}$	4.155	4.782	2.532	3.089
$H_2/4H_1$	0.216	0.217	0.201	0.212
$\frac{1}{2}F \,/\, \sqrt{[D(H_1-H_2)]}$			0.335	0.453
$(4DH_1)^{\frac{1}{2}} + F \,/\, (4DH_1)^{\frac{1}{2}} - F$			1.347	1.429

TABLE 4-30

Components of variation for 1000 corn weight in two seasons, 9 x 9 half diallel, 2-rowed genotypes, data from F_1 and F_2 pooled

	1970 Blocks		1971 Blocks	
Component	I	II	I	II
D	11.392 ± 0.734	5.105 ± 0.898	25.874 ± 0.655	17.980 ± 1.589
H_1	7.343 ± 2.958	8.545 ± 3.621	18.111 ± 2.638	30.988 ± 6.406
H_2	6.726 ± 2.895	6.023 ± 3.544	17.770 ± 2.582	30.307 ± 6.270
F	4.690 ± 1.984	0.417 ± 2.428	9.003 ± 1.769	6.037 ± 4.296
E_o	1.604 ± 0.520	1.526 ± 0.637	2.732 ± 0.464	4.410 ± 1.126
E_1	2.567 ± 0.480	2.251 ± 0.587	3.899 ± 0.428	3.527 ± 1.039
E_2	2.231 ± 0.392	3.375 ± 0.480	4.387 ± 0.349	6.303 ± 0.848
$(H_1/D)^{\frac{1}{2}}$	0.803	1.294	0.837	1.313
$H_2/4H_1$	0.229	0.176	0.245	0.245
$\frac{1}{2}F/\sqrt{[D(H_1-H_2)]}$	0.885		1.516	
$(4DH_1)^{\frac{1}{2}} + F /(4DH_1)^{\frac{1}{2}} - F$	1.689		1.525	

values of the ratio $\frac{1}{2}F / \sqrt{[D(H_1-H_2)]}$, obtained in the data for 1971, would suggest that the ratio of h to d was not consistent over all loci and the positive values of F, together with values for the quantity $(4DH_1)^{\frac{1}{2}} + F/(4DH_1)^{\frac{1}{2}} - F$ of more than 1 indicate a greater proportion of dominant than recessive alleles in the inbred lines.

The estimates of D, H_1, H_2, F, E_o, E_1 and E_2 were used to reconstruct expected values for the twelve statistics and analysis of their deviation from the observed values was performed. The overall deviation item was found to be significant in both seasons and indicated a failure of the model due to epistasis.

When the components were estimated for the 2-rowed population only (table 4-30) the situation was quite different. Complete dominance was indicated with approximately equal gene frequencies. The overall deviation of observed from expected for the statistics was not significant in either season and this confirmed the results of previous analyses that epistasis occurred almost entirely in crosses between 6-rowed and 2-rowed parents.

The analysis of variance for combining ability was performed on the 1971 data for the 13 x 13 half diallels and the 9 x 9 diallels comprising 2-rowed genotypes only. Significant items were detected for both general and specific combining ability (table 4-31).

The g.c.a. and s.c.a. effects are given in tables 4-32 and 4-33. For the 13 x 13 half diallel both s.c.a. and g.c.a. were extremely consistent between blocks

TABLE 4-31

Combining ability analyses for 1000 corn weight, 1971

	13 x 13				9 x 9 2-rowed genotypes			
		Blocks				Blocks		
		I	II			I	II	
Item	D.F.	M.S.	M.S.		D.F.	M.S.	M.S.	
General combining ability	12	118.392 ***	75.629 ***		8	30.030 ***	23.956 ***	
Specific combining ability	65	152.738 ***	150.669 ***		27	6.851 **	8.041 **	
Error		3.730 (698 d.f.)	4.586 (696 d.f.)			3.561 (323 d.f.)	3.908 (323d.f.)	

TABLE 4-32

General ($\hat{g}_i$) and specific ($\hat{s}_{ij}$) combining ability effects for 1000 corn weight, 13 x 13 half diallel F_1, 1971

	$\hat{s}_{ij}$												$\hat{g}_i$	
	2	3	4	5	6	7	8	9	10	11	12	13	I	II
1	-16.805	2.287	6.663	3.343	-4.441	-18.676	4.808	4.942	0.977	5.436	6.876	4.592	2.883	2.149
	-18.492	3.236	6.605	4.191	-2.122	-19.614	4.148	2.660	3.489	3.443	3.994	8.461		
2		2.257	2.033	2.292	-5.222	-16.927	5.637	1.601	6.027	5.895	6.615	6.601	4.024	3.576
		3.250	3.128	3.045	-5.638	-13.771	3.312	3.054	8.013	6.816	5.097	2.195		
3			0.355	-2.916	0.500	3.985	0.609	-1.597	-0.982	1.157	-3.033	-2.617	-0.697	0.258
			-5.374	-0.837	3.140	7.687	-1.390	-2.008	2.021	-3.975	-3.864	-1.887		
4				-0.430	0.807	7.541	-2.584	-1.131	-3.795	-2.097	-4.197	-3.161	0.286	-0.810
				-2.489	0.178	8.446	-4.152	2.060	-1.021	0.443	-3.976	-3.849		
5					2.316	4.730	-3.625	0.978	1.514	-4.578	-1.728	-1.892	-1.403	-1.197
					1.965	4.722	-1.985	-1.623	-0.134	-8.161	-0.420	1.727		
6						-8.073	5.731	1.295	3.690	2.778	0.078	0.555	-8.309	-6.194
						-11.521	4.962	0.724	1.653	3.397	0.287	2.975		
7							4.316	7.149	5.675	3.253	2.163	4.869	1.416	1.809
							4.589	6.881	1.260	5.904	3.015	2.402		
8								-0.616	-10.151	-1.443	-1.743	-0.936	-1.238	-1.404
								0.754	-7.847	-1.793	0.757	-1.355		

TABLE 4-32 Cont'd

General ($\hat{g}_i$) and specific ($\hat{s}_{ij}$) combining ability effects for 1000 corn weight, 13 x 13 half diallel F_1, 1971

							$\hat{s}_{ij}$					$\hat{g}_i$	
2	3	4	5	6	7	8	9	10	11	12	13	I	II
9								0.473	-8.079	-0.969	-4.043	1.218	1.934
								-4.155	-5.022	0.709	-4.033		
10	Block I population mean ($\hat{u}$) = 50.33 ± 0.219								0.047	-0.903	-2.557	-2.147	-2.035
	S.E. ($\hat{s}_{ij}$) = 1.763								1.947	-1.742	-3.484		
11										-2.055	-0.309	-1.185	-1.649
										-1.858	-1.141		
	Block II population mean = 48.78 ± 0.242										-1.099	0.484	0.690
12	S.E. ($\hat{s}_{ij}$) = 1.955										-2.000		
13												4.668	2.873
										S.E. ($\hat{g}_i$-$\hat{g}_j$)		± 0.823	± 0.913

TABLE 4-33

General ($\hat{g}_i$) and specific ($\hat{s}_{ij}$) combining ability effects for 1000 corn weight, 9 x 9 half diallel F_1, 2-rowed genotypes, 1971

	$\hat{s}_{ij}$							$\hat{g}_i$	
	4	5	8	9	10	11	12	13	I	II
3	1.574	-2.321	2.321	-0.672	0.139	2.421	-2.002	-1.459	0.241	0.192
	-2.819	1.084	0.973	-0.173	4.013	-1.249	-2.162	0.334		
4		1.311	0.272	0.939	-1.529	0.312	-2.021	-0.858	0.080	-1.025
		-0.419	-1.640	4.044	1.120	3.318	-2.125	-1.479		
5			-1.392	2.425	3.156	-2.792	-0.175	-0.212	-0.986	-0.778
			-0.108	-0.273	1.372	-5.919	0.798	3.464		
8				1.946	-7.392	1.459	0.926	1.859	-1.937	-1.426
				2.545	-5.899	0.890	2.417	0.823		
9					2.445	-5.964	0.914	-2.034	1.306	2.439
					-2.735	-2.866	1.841	-2.383		
10	Block I population mean ($\hat{u}$)					2.358	1.175	-0.352	-2.256	-1.686
	= 48.38 ± 0.314					4.260	-0.453	-1.677		
11							0.166	2.039	-1.437	-2.035
	S.E. ($\hat{s}_{ij}$) = ± 1.634						0.165	1.401		
12								1.016	0.466	1.328
	Block II population mean ($\hat{u}$)							-0.482		
13	= 46.50 ± 0.329								4.523	2.992
	S.E. ($\hat{s}_{ij}$) = ± 1.712							S.E. ($\hat{g}_i - \hat{g}_j$)	± 1.009	± 1.057

($r = 0.9113$, $P < 0.001$ and $r = 0.9705$, $P < 0.001$ respectively). Negative s.c.a. effects were found for all crosses between 6-rowed parents and for most crosses between 2-rowed parents. Large positive effects were frequent for crosses between 2-rowed and 6-rowed parents. Whereas three of the four 6-rowed parents showed high positive g.c.a., Scotch Bere exhibited high negative g.c.a. The largest positive g.c.a. effects associated with a 2-rowed parent were those for Boreham Warrior. This was also the case when the population containing only 2-rowed genotypes was analysed (table 4-33). Positive g.c.a. effects were also shown by Cambrinus (3), Maris Baldric (9) and Sultan (12). Golden Promise (8) and Midas (10) showed negative g.c.a., and large negative s.c.a. effects were found for both blocks for the cross between them. On the other hand the cross between Midas and Mosane (11) showed a relatively high and consistent positive effect.

The correlation between blocks for g.c.a. was again close ($r = 0.8991$, $P < 0.001$) whilst that for s.c.a. was somewhat lower ($r = 0.5340$, $P < 0.001$).

CHAPTER 5

GENERAL DISCUSSION ON PART I

The diallel cross analyses used in this investigation depend for their validity on the following basic assumptions:

1) diploid segregation ;
2) absence of reciprocal differences ;
3) independent action of non-allelic genes ;
4) no multiple allelism ;
5) homozygous parents ;
6) genes independently distributed.

(Hayman, 1958)

The first assumption may be taken for granted since, as has already been noted in Chapter 1, development of the barley crop has been entirely at the diploid level.

The presence or absence of reciprocal differences between crosses was tested by the c and d items in the analysis of variance of the 9 x 9 full diallels and such differences were detected in a number of cases. However, conclusions were largely drawn from analyses of the larger 13 x 13 half diallel sets in which the mean values for crosses were averaged over reciprocals where these had been grown (see Chapter 3).

Several tests were used to check the adequacy of the model, which assumes a simple additive-dominance situation with independent gene distribution, no non-allelic interaction and no multiple allelism. Thus any of the following

findings indicated a failure of the model:

1) departure of Wr, Vr regression line from unit slope;
2) heterogeneity of Wr-Vr values when tested over blocks;
3) failure of the estimated components of variation (D, H_1 H_2 etc.) to adequately account for the variation observed in the experiment.

It should be noted that under certain conditions non-allelic interaction (epistasis) may remain undetected by the W/V analysis. Duplicate interaction may sometimes be difficult to detect from the Wr, Vr regression (Jana and Seyffert, 1972). Again, in the presence of either i type (homozygote x homozygote) interaction or l type (heterozygote x heterozygote) interaction alone, the points scatter along a line of unit slope even in the absence of dominance (Jinks and Mather, 1971).

Seed for the parents used in this study was taken from breeder's stocks and homozygosity was assumed. The similarity in most cases for the characters analysed of the average parental and F_1 within-family variances, E_o and E_1, when compared to the usually much larger average within-family variance of the F_2 generation, E_2, provided some confirmation of this assumption. However, heterogeneity of rachilla hair length was detected in the Deba Abed stock after completion of the experiments though no other morphological heterogeneity was apparent in this or any of the other parents.

Since all the parents under investigation have been subjected to selection for various characters, it might

perhaps be expected that the distribution of genes for all characters might not be independent. However, the parents represent a wide range in origin, pedigree, and mean expression of the characters measured so that it is unlikely that such gene association or dispersion as might have resulted from selection would seriously affect the validity of the analyses. However, results described in Chapter 6 suggested that some parents were difficult to distinguish when several traits, including the components of yield, were considered simultaneously.

The Experimental Design

It was pointed out by Mather and Jinks (1971) that the first requirement of any experiment in continuous variation is that it should supply a measure of the non-heritable variation to which the individuals under test are subject and a means of separating this from the heritable component of variation. In experiments where the individuals of a family are grown together in plots the estimation of the non-heritable variation between families requires adequate replication and is considered separately from the non-heritable variation within families which is the average intra-plot variance.

In the experiments reported here plants were sown, and later set out in the field, in individually randomized positions so that plots, as such, did not exist and a common E was estimated from the differences among the individuals of the genetically uniform families. Thus

the non-heritable component of differences between the means of families each of n plants was E/n.

In the absence of genotype-environment interactions or competition effects it was expected that the within-family variances for the F_1 generation and parents would have been homogeneous. This was found not to be the case however and heterogeneity of variances was detected for all the traits analysed. Correlation coefficients for the means and variances of the thirteen parents for the three yield components are shown below.

Correlations of variances of parents and their means for characters in two seasons

n = 13

Season	Block	Tiller no.	Grains/ear	Corn weight
1970	I	0.5128 N.S.	0.8095 ***	0.8573 ***
	II	0.7892 **	0.5585 *	0.2873 N.S.
1971	I	0.6235 *	0.7794 **	-0.2438 N.S.
	II	0.6480 *	0.5748 *	0.2540 N.S.

The only trait for which no consistent relationship could be shown was corn weight. In the case of the other two traits, inspection of the data showed that the positive correlations between the parental means and their variances were almost entirely due to the contrast between the 6-rowed and the 2-rowed genotypes. Thus the 6-rowed genotypes produced fewer tillers than the 2-rowed genotypes and exhibited much lower variances. In addition the 6-rowed genotypes were highly variable for grains per ear by comparison with the 2-rowed genotypes. The genotype-

environment interaction was usually removed or much reduced when the 2-rowed population alone was considered. All the analyses however were conducted on untransformed data from both the 13 x 13 diallel sets (2-rowed + 6-rowed) and the 9 x 9 diallel sets containing only 2-rowed genotypes.

The rather small family size, particularly for the F_2 generation, of ten sibs only, was perhaps a weakness in the experimental design but this was a consequence of the immense labour involved not only in producing large quantities of hybrid seed by hand pollinations in barley, but also in sowing the experiment and recording the observations. On the whole a reasonable balance appears to have been made between family size and the number of parents which could be included in the experiment.

Correlation coefficients for the comparisons between blocks and between mean values for seasons of parental values for the three yield components and yield itself are shown in table 5-1. It was not found possible to obtain accurate direct measurements of yield per plant because unavoidable damage at harvest sometimes led to ear loss or grain loss. The best estimate of yield was obtained as the product of the three components but, as can be seen from the table, the estimates were not consistent between blocks or between seasons. This being the case, and since for a complex character such as yield, accurate estimates from only ten plants per family could not really be expected, no further analyses were conducted

TABLE 5-1

Correlation coefficients for the comparisons between blocks and seasons of the three components of yield and their product

		Tiller Number	Grains per ear	1000 corn weight	Yield
Between blocks	1970	0.8236 ***	0.9402 ***	0.6823 *	0.4665 N.S.
	1971	0.9362 ***	0.9216 ***	0.8892 ***	0.2764 N.S.
Between years		0.7208 **	0.9787 ***	0.6479 *	0.0287 N.S.

n = number of pairs of observations = 13

on yield as estimated. In this connection, Immer (1942) studied the distribution of yields of single plants of varieties and F_2 crosses in barley and concluded that the yield of single plants is determined largely by environmental factors.

Highly significant correlations were obtained for all other comparisons with the exception of that between blocks in 1970 and that between seasons for 1000 corn weight. The conclusions drawn from analyses of this trait were mainly based on the data from 1971. It seems clear that environmental effects were responsible for the low corn weights obtained in the 1970 experiment (see table 4-23) and that the potential genetic expression of the trait was to a large extent prevented. No such obvious seasonal effect was found for the other yield components though expression was higher in the second season.

The Genetic Analyses

Heritability estimates were computed from the components of variation and are shown in tables 5-2a and 5-2b. The estimates were lower for all three traits in the 2-rowed population, reflecting presumably the narrower range of expression in this population compared with that containing both 6-rowed and 2-rowed genotypes.

The difference between heritability in the broad sense and heritability in the narrow sense, estimated for the same material, is directly proportional to the

TABLE 5-2

Narrow and broad sense heritability estimates, computed from the components of variation, for the three components of yield

a) 13 x 13 2-rowed + 6-rowed population

	tiller number				grains per ear				1000 corn weight			
	1970		1971		1970		1971		1970		1971	
	I	II	I	II	I	II	I	II	I	II	I	II
Broad heritability	0.69	0.67	0.59	0.61	0.84	0.87	0.88	0.90	0.95	0.92	0.91	0.89
Narrow heritability	0.62	0.50	0.53	0.45	0.33	0.33	0.60	0.56	0.25	0.29	0.33	0.22

b) 9 x 9 2-rowed population

	I	II	I	II	I	II	I	II	I	II	I	II
Broad heritability	0.32	0.45	0.45	0.43	0.50	0.67	-	0.60	0.68	0.69	0.77	0.80
Narrow heritability	0.10	0.21	0.23	0.06	0.23	0.30	-	0.33	0.46	0.49	0.51	0.36

$$\text{Broad heritability} = \frac{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - \frac{1}{2}F}{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - \frac{1}{2}F + E_1}$$

$$\text{Narrow heritability} = \frac{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{2}H_2 - \frac{1}{2}F}{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - \frac{1}{2}F + E_1}$$

influence of non-additive genetic variance in the inheritance of the character under study. Thus for the trait tiller number little non-additive genetic variance was apparent in the 13 x 13 diallel sets whereas it was clearly operative in the 9 x 9 2-rowed diallel sets. Considerable non-additive genetic variance was indicated for the other two traits in both populations.

Productive tiller number

The genetic analyses on the component productive tiller number were to some extent obscured by the effect of environment. The lower variances associated with crosses between 6-rowed genotypes than with crosses between 2-rowed genotypes may have been a reflection of the greater capacity of the 2-rowed types to respond to environmental fluctuations by tillering to a greater or lesser extent. This was also noted by Johnson and Aksel (1959).

Such non-additive genetic variance as was detected in the F_1 was not detectable in the F_2 data at least for 1971. Directional dominance could not be found in the 13 x 13 diallel sets when the correlation between $\underline{y}_r$ and Wr+Vr was computed but its presence was indicated by the significance of the $\underline{b}_1$ item in the Hayman analysis of F_1 data for 1971. The Wr, Vr graphs indicated partial dominance in both seasons and the Boreham Warrior array consistently occupied the recessive end of the regression line. The clustering of the points representing 6-rowed

parental arrays towards the dominance end of the line was no doubt the reason for the failure to detect unidirectional dominance though it was found on analysis of the 6-rowed genotypes only and the 2-rowed genotypes only that dominance within these populations was acting in the direction of increased tiller production. It appears therefore that in the 2-rowed and in the 6-rowed populations dominance was acting in the same direction but at different levels of phenotypic expression.

The predominantly additive nature of the inheritance in the 13 x 13 diallel was confirmed by the highly significant item for general combining ability in each of the four analyses shown in table 4-9, whereas that for specific combining ability was significant only at the 5% level of probability in two of the analyses and not significant at all in the other two. The general combining ability effects were found to be consistent between blocks and seasons (tables 4-10 and 4-11). Further, no interaction was found between years and additive genetic effects in the Hayman analyses (tables 4-4 and 4-5) whereas significant interactions of b items with years were detected.

Heterosis was detected in several crosses but only a few of these displayed epistasis (tables 4-6a and 4-6b).

Grains per ear

Although a clear confirmation of the dominance of the 2-rowed expression, in hybrids between 2-rowed and

6-rowed parents, was demonstrated there appeared to be marked differences in the levels of variation within the 2-rowed and 6-rowed populations. Relatively high variances within the 6-rowed population were not entirely unexpected since some of the 6-rowed material was found to be prone to shattering of the ear which led to some losses during harvest. Whenever possible the loss of part of a spike was taken into account but some inflation of variance was probably inevitable.

The same explanation might be given for the heterogeneity of variance within the 2-rowed by 6-rowed hybrid population, since the hybrids, whilst having 2-rowed spikes may have inherited the brittleness of the rachis associated with some of the 6-rowed parents. The possibility of a genetic explanation cannot be ruled out since analysis of the coefficients of variation, computed for each family, indicated significant additive and non-additive components of variation. Brittleness might be associated with earliness in the sense that the early genotypes would be "over-ripe" and thus prone to shattering, by the time the trials were harvested. The 6-rowed genotypes were earlier, in terms of days to heading, than the 2-rowed genotypes and exhibited dominance for this character (Riggs and Hayter, 1972).

The data exhibited a high level of non-additive genetic variation and the 2-rowed population showed significant $\underline{b}_1$ items in the analyses of variance (table 4-14). This item tests the mean deviation of the F_1's

from the mid-parental values, and the hybrids exceeded the mid-parents by an average of 10.5% in 1970 and 7.4% in 1971. Considering only those crosses which exhibited heterosis, the average increase over the better parents was 8.6% in 1970 and 5.9% in 1971 (tables 4-15a and 4-15b), whilst for the whole population of 2-rowed genotypes the average heterosis was 4.0% and 1.6% in 1970 and 1971 respectively.

The order of dominance, acting in the direction of low numbers of grains per ear, detected in the complete data supported the results of Johnson and Aksel (1959) but when 2-rowed genotypes only were analysed at F_2, dominance was found to be acting towards higher number of grains. These findings agreed with those of Hayes (1965) but not with those of Johnson and Aksel (loc cit).

The detection of large additive effects in the inheritance of this trait suggests that no difficulty should be experienced by the breeder in attempting to fix the desired expression. The demonstration of interaction between additive effects and seasons implies, however, that general combining ability effects estimated in one season only may be an inadequate basis for decision making. The detection of a positive correlation between g.c.a. effects for 2-rowed genotypes and the corresponding parent expression of the trait suggests a further aid in the choice of parents.

1000 corn weight

The effect of environment on the expression of this trait was demonstrated by the considerably higher values obtained in 1971 compared to those for 1970 (table 4-23) and the analyses suggested that the true genetic relationships were in some cases obscured by unfavourable environmental factors in the first season.

The most striking result of these analyses was the demonstration of over-dominance in the population containing both 6-rowed and 2-rowed genotypes. Removal of the 6-rowed genotypes from the analysis resulted in a situation showing complete dominance and no interaction. Since the epistasis detected by other tests was almost confined to crosses between 2-rowed and 6-rowed genotypes, the apparent over-dominance was perhaps a spurious inflation of dominance caused by epistasis (Jinks, 1955).

Heterosis occurred in a large number of crosses and in the second season an average increase of 18.5% over the mean of the better parents was measured. The average heterotic increase was larger in 1970 but was perhaps a less accurate measure. Few of the crosses showing heterosis showed evidence of epistasis (tables 4-28a and 4-28b), and since over-dominance was not demonstrated in the absence of epistasis, the heterosis was presumably the result of bringing together in the hybrid the dominant favourable genes of both parents (Jones, 1917).

Jinks and Jones (1958) stated that there is a correlation between the presence or absence of heterosis and the presence or absence of non-allelic interactions, and while heterosis can arise in the absence of non-allelic interactions, it does so with a lower frequency and a lower mean expression. Whilst in these data heterosis occurred in a large number of crosses for which epistasis could not be demonstrated, the mean heterotic expression was slightly higher for the epistatic crosses which, as previously remarked, were almost entirely confined to 2-rowed by 6-rowed parental combinations. Interaction resulting in heterosis may be between homozygous/homozygous or homozygous/heterozygous combinations (Jinks and Jones, loc cit) but the data were insufficient to determine which type of interaction was involved here.

It is known (e.g. Lambert and Liang, 1952) that the lateral grains in 6-rowed genotypes are usually smaller and lighter than the median grains. Thus the average corn weight of these genotypes is generally lower than that for 2-rowed genotypes. Hybrids between the two types produce, in the F_1, ears in which the lateral florets usually do not set grain so that measurement of corn weight in the F_1 takes account only of median grains. Further, the expression, in the hybrids, of factors presumably present in 6-rowed genotypes, which determine the ability of the plant to store more carbohydrate assimilate per ear than is normal in 2-rowed genotypes, may not be fully suppressed. This might explain why the

corn weights for such hybrids are higher than those for hybrids between 2-rowed parents. The non-allelic interaction detected in hybrids between 2-rowed and 6-rowed genotypes may have been between the Vv locus, for 6-rowed vs 2-rowed expression, and genes influencing movement or storage of carbohydrate.

The "local" 6-rowed variety, Scotch Bere, did not exhibit such marked heterosis when crossed to 2-rowed parents as did the other 6-rowed varieties, and the point representing the Scotch Bere array was nearest to those representing the arrays of 2-rowed parents in the Wr, Vr graph (figure 4-12).

Golden Promise and Midas, which are both derived from an induced mutant of Maythorpe, were identified as unusual genotypes with respect to corn weight (figure 4-15) and exhibited an excess of recessive genes (figures 4-14, 4-15, 4-16).

Correlations Between Traits

The variances and covariances for the three yield components and for time to heading, all for the F_1 generation, were partitioned into the average within-family and the between-family components. For this purpose data from the two blocks were pooled. Subtraction of the average within-family variance-covariance matrix from the between-family variance-covariance matrix gave the matrix corresponding to genetic variances and covariances freed from environmental effects.

Phenotypic, genotypic and environmental correlation coefficients for the four traits are shown in table 5-3 for the 13 x 13 F_1 diallels and in table 5-4 for the 9 x 9 F_1 diallels comprising 2-rowed genotypes only. Appropriate tests of significance for genotypic correlations have not been developed.

The contrast between tables 5-3 and 5-4 is striking. Few of the phenotypic correlations reached significance for the 2-rowed population whereas only one correlation failed to reach significance when the population containing 2-rowed and 6-rowed genotypes was considered.

The significant positive phenotypic association between tiller number and time to heading shown in table 5-3 was of similar magnitude in both seasons, as was the genetic association, and indicated increased tiller number associated with late heading. On the other hand, when 2-rowed genotypes alone were considered, a tendency was revealed for the earlier genotypes to produce more tillers. Aksel and Johnson (1961) found no relationship between sowing-to-heading period and the number of ears per plant in a 6-parent diallel cross of 6-rowed parents only. Hayes (1965), on the other hand, reported a tendency for the early genotypes, in terms of days to heading, to produce more heads per plant in a 10-parent diallel of 2-rowed parents when plants at F_1 were space-planted. Fiuzat and Atkins (1953) noted negative correlations between time to heading and number of heads in crosses between four 6-rowed parents but pointed out that this high association would be of little value in

TABLE 5-3

Phenotypic, genotypic and environmental correlation coefficients between four traits in each of two seasons for the 13 x 13 F_1 half diallels

Traits	phenotypic		genotypic		environmental	
	1970	1971	1970	1971	1970	1971
	n = 91					
time / tiller no.	0.4340 ***	0.4173 ***	0.5227	0.5054	-0.2584 ***	-0.2347 ***
time / grains per ear	-0.3262 **	-0.2807 **	-0.3401	-0.2932	-0.0743 *	-0.0705 *
time / corn weight	-0.3149 **	-0.2065 *	-0.3168	-0.2115	-0.2780 ***	-0.0909 **
tiller no. / grains per ear	-0.3670 ***	-0.4145 ***	-0.4379	-0.4939	0.1154 ***	0.0452 N.S.
tiller no. / corn weight	-0.4353 ***	0.0476 N.S.	-0.5164	0.0503	0.1456 ***	0.0422 N.S.
grains per ear / corn weight	-0.3235 **	-0.5641 ***	-0.3570	-0.6060	0.2414 ***	0.1009 **

time = time to heading

TABLE 5-4

Phenotypic, genotypic and environmental correlation coefficients between four traits in each of two seasons for the 9 x 9 F_1 half diallels comprising 2-rowed genotypes only

Traits	phenotypic		genotypic		environmental	
	1970	1971	1970	1971	1970	1971
	n = 45					
time / tiller no.	-0.3029 *	-0.2181 N.S.	-0.4133	-0.2274	-0.2403 ***	-0.2186 ***
time / grains per ear	0.2198 N.S.	0.4955 ***	0.3067	0.6600	-0.1123 **	-0.1171 **
time / corn weight	-0.0121 N.S.	0.0946 N.S.	0.0203	0.1282	-0.2251 ***	-0.1530 ***
tiller no. / grains per ear	-0.0751 N.S.	0.1299 N.S.	-0.3012	0.1024	0.1774 **	0.1900 ***
tiller no. / corn weight	-0.0869 N.S.	0.3663 *	-0.2654	0.4500	0.1884 ***	0.1084 **
grains per ear / corn weight	0.2841 N.S.	0.4403 **	0.2469	0.4432	0.4149 ***	0.4921 ***

time = time to heading

individual plant selection because number of heads had a very low heritability. On the other hand Grafius (1959) showed that earliness tended to prevent full expression of potential tillering capacity of the genotype. Six-rowed spring barley was used in this work and the superiority of the F_1 hybrids over the parents, in terms of the number of heads per plant, increased with lateness.

The detection of a strong positive association between yield and number of heads per plant and between yield and plant height, together with a negative association between time to heading and number of heads and between time to heading and height led Fiuzat and Atkins (loc cit) to suggest selection for early and tall genotypes. Although no evidence for the relationships between the yield components and height is given for the material studied here, these selection criteria are in direct contrast with those suggested by experience under Scottish conditions. The 2-rowed parents included in this study were generally later, in terms of days to heading, than the 6-rowed parents (Riggs and Hayter, 1972) and they produced relatively more tillers (table 4-1). Johnson and Aksel (1959) also noted the high tillering propensities of 2-rowed materials in their study. The positive association between time to heading and tiller number shown in table 5-3 is almost certainly due to the low tillering capacity of the early 6-rowed genotypes. Amongst the 2-rowed material, however, the earlier genotypes tended to produce more tillers but the association

was not a strong one.

The significant negative environmental correlation coefficients for time to heading and tiller number in both tables suggest that the environmental conditions favouring early heading favoured high tiller production. This was also the case for the traits grains per ear and corn weight and confirms the findings of Fiuzat and Atkins (loc cit).

The negative phenotypic and genotypic correlations between time to heading and grains per ear in the 13 x 13 diallels for both seasons may again perhaps be attributed to the 6-rowed genotypes, which, as has been noted above, were earlier than the 2-rowed genotypes. Amongst these latter (table 5-4) positive correlations were detected between the two traits and the phenotypic correlation for 1971 was highly significant. Reference to table 4-11 reveals that the two latest 2-rowed parents, Midas and Boreham Warrior (Riggs and Hayter, loc cit) produced the highest number of grains per ear in 1971 though this was not so marked in 1970.

It was remarked earlier in this chapter that considerable heterosis for 1000 corn weight occurred in crosses between 6-rowed and 2-rowed genotypes. This is almost certainly the explanation for the significant negative phenotypic correlations between time to heading and corn weight in the 13 x 13 diallels. No correlations were found between these traits in the 2-rowed population.

In general, for the adapted 2-rowed genotypes, time

to heading was of no marked significance in the expression of the three components of yield. The significant correlations of these components with time to heading demonstrated in table 5-3 were largely due to the contrast between the low tillering capacity, high number of grains per ear and low corn weight of the early heading 6-rowed parents, and the later heading 2-rowed parents, with higher tillering capacity, fewer grains and higher corn weights (tables 4-1, 4-11 and 4-23).

Phenotypic correlations between the yield components themselves again showed differences between the populations containing both 2-rowed and 6-rowed genotypes and those containing only 2-rowed genotypes. The correlations between the components for the 13 x 13 diallel could generally be explained in terms of the basic differences between 2-rowed and 6-rowed genotypes whilst for the 2-rowed population the phenotypic correlations were mostly not significant, but in 1971 both tiller number and grains per ear were positively correlated with corn weight.

Almost all the phenotypic correlations in both tables were so similar to the corresponding genotypic correlations that they can be safely regarded as reflecting the true genetic relationships.

The environmental correlations were positive and mostly significant for the relationships between the three yield components indicating that environmental fluctuations affected the expression of these traits in

the same direction.

When the F_2 data were analysed in the same way (tables 5-5 and 5-6), broadly similar relationships between the traits were revealed as for the F_1 data.

The number of tillers and the number and weight of grains produced by a plant may be partly determined by the size or weight of the grain from which it was grown. In order to examine this possibility the phenotypic correlations between corn weight of the F_1 and the expression of the three yield components at F_2 were computed for the 1971 data (table 5-7). Corn weight at F_1 and corn weight at F_2 were highly correlated both for the 13 x 13 half diallels and for the 9 x 9 half diallels comprising 2-rowed genotypes only. This confirmed the high heritability of the trait 1000 corn weight already noted in tables 5-2a and 5-2b. The only other significant correlation was that between corn weight at F_1 and number of grains per ear at F_2 for the 13 x 13 diallels. This negative correlation was undoubtedly due to the presence of the 6-rowed genotypes and no such correlation was found for the 9 x 9 diallels. There was therefore no direct relationship between weight of grain sown and the expression of the other two components of yield at least in the 2-rowed population.

It should be borne in mind that all the correlations discussed above apply to a population of which the parents have mostly been produced as a result

TABLE 5-5

Phenotypic, genotypic and environmental correlation coefficients between four traits in each of two seasons for the 13 x 13 F_2 half diallels

Traits	phenotypic		genotypic		environmental	
	1970	1971	1970	1971	1970	1971
	n = 91					
time / tiller no.	0.0222 N.S.	0.3439 ***	0.0529	0.5006	-0.2584 ***	-0.2348 ***
time / grains per ear	-0.4907 ***	-0.4790 ***	-0.5111	-0.5072	-0.0743 *	-0.0706 *
time / corn weight	-0.4195 ***	0.1079 N.S.	-0.4352	0.1248	-0.2780 ***	-0.0909 **
tiller no./ grains per ear	-0.5549 ***	-0.5740 ***	-0.6715	-0.7871	0.1154 ***	0.0452 N.S.
tiller no./ corn weight	-0.2770 **	0.3356 **	-0.3673	0.4498	0.1457 ***	0.0423 N.S.
grains per ear/ corn weight	0.0939 N.S.	-0.4730 ***	0.0810	-0.5345	0.2414 ***	0.1009 **

time = time to heading

TABLE 5-6

Phenotypic, genotypic and environmental correlation coefficients between four traits in each of two seasons for the 9 x 9 F_2 half diallels comprising 2-rowed genotypes

Traits	phenotypic		genotypic		environmental	
	1970	1971	1970	1971	1970	1971
	n = 45					
time / tiller no.	-0.3226 *	-0.0789	-0.4218	0.0133	-0.2404 ***	-0.2187 ***
time / grains per ear	0.0687 N.S.	0.5401 ***	0.1166	0.8419	-0.1123 **	-0.1171 **
time / corn weight	-0.2190 N.S.	0.1345 N.S.	-0.2234	0.1852	-0.2251 ***	-0.1530 ***
tiller no. / grains per ear	0.0051 N.S.	-0.0572 N.S.	-0.1414	-0.6418	0.1774 **	0.1900 ***
tiller no / corn weight	0.0231 N.S.	0.2367 N.S.	-0.0731	0.5860	0.1884 **	0.1085 **
grains per ear / corn weight	0.2412 N.S.	0.2825 N.S.	0.1731	0.2349	0.4150 ***	0.4921 ***

time = time to heading

TABLE 5-7

Phenotypic correlation coefficients for the relation between corn weight at F_1 and the expression of the three components of yield at F_2 1971 data

Components	13 x 13 half diallel 2-rowed + 6-rowed (n = 78)	9 x 9 half diallel 2-rowed (n = 36)
1000 corn weight F_1 and :		
1000 corn weight F_2	0.7556 ***	0.6150 ***
tiller number F_2	0.0895 N.S.	0.1130 N.S.
grains per ear F_2	-0.3143 **	0.1815 N.S.

of conscious selection by plant breeders. The parents are fairly diverse, but nevertheless these correlations may not be found in an unimproved population of barley.

Practical Applications

Dudley and Moll (1969) pointed out that the more diverse the sample of environments under which experiments are conducted the smaller the estimate of genetic variance, since more of the genotype x environment interaction variance is removed. They point out a) that the estimates of genetic variance used in making decisions on selection procedure should, so far as possible, be free of genotype x environment interaction and b) the heritability value should be computed on the basis of the type of selection unit (including numbers of replications, years, locations, types of progenies and plots) which will be used in the selection programme for which progress is being predicted. This aspect in the computation of heritability estimates was also stressed by Hanson (1963).

The pedigree selection method employed by the author at the Scottish Plant Breeding Station involves initial selection of single F_2 plants spaced at 9" between rows and 2" within rows. This spacing is very similar to that employed in the diallel experiments. The heritability estimates obtained from the experiments should thus be relevant to the procedure employed in the

early stages of selection, with the proviso that the absolute values of the estimates for the three traits will vary over seasons.

The type of genetic variance to be included in the numerator of a heritability estimate depends upon the type of selection to be practised and the plant material and mode of reproduction of the crop (Hanson, loc cit). When progress is referenced to heritability estimates derived from F_2 plants of an inbreeding crop such as barley, the numerator should include only additive genetic variance and the additive x additive component of epistasis. This is because the variability due to dominance is negligible in advanced progeny rows.

Looking at the problem simply, an experienced plant breeder can perhaps rank a series of characters on their response to selection. Heritability offers an objective numerical confirmation. Considering the narrow-sense heritability estimates from the 2-rowed population (table 5-2b), the effectiveness of selection is expected to be fairly high for corn weight, less so for grains per ear and rather low for tiller number.

In order to assess the potential of the various parental combinations to produce homozygous lines exhibiting high expression of one or more of the components of yield, it is useful to consider the means and genetic standard deviations of the individual crosses.

In this investigation the within-family variances were estimated for each cross in the F_1 and F_2 generations.

Thus, subtraction of E_1, the average within-family variance of the F_1 and so a measure of the environmental variance, from each F_2 family variance should give an estimate of the genetic variance for each F_2 family. However, the previously demonstrated heterogeneity of variances reduces the validity of such a procedure and instead the genetic standard deviation for the F_2 mean of each cross was derived from the difference between the individual variances for the F_1 and F_2 generations. Both means and variances were based on the family size of 20 plants achieved by pooling data from the two blocks. In cases where the F_1 variance equalled or exceeded the F_2 variance, the genetic variance was recorded as zero. The F_2 means and their genetic standard deviations for the three traits are given in tables 5-8, 5-9, 5-10, 5-11, 5-12. Data from both seasons are presented except in the case of 1000 corn weight for which only the data for the second season were considered.

The 5% fiducial limits for the genetic deviations can be obtained by multiplying the deviation by the appropriate value of $\underline{t}$, which in this case is 1.729 for the one-tailed test. For example, the upper limit of the range which might be achieved by segregates of the cross 1 x 2 for 1000 corn weight in 1971 is 36.7 + (1.729 x 5.75) = 46.6.

It is not necessary, for the estimation of the means and variances described above, that a diallel

TABLE 5-8

Productive tiller no: means and genetic standard deviations, F_2, 1970 data

		1	2	3	4	5	6	7	8	9	10	11	12	13
1	Olli	2.20												
2	Pirkka	2.08 ±0.983	2.05											
3	Cambrinus	3.09 ±0.167	3.00 ±1.046	3.20										
4	Ymer	3.85 ±1.340	2.75 ±0.000	3.80 ±0.000	3.85									
5	Deba Abed	3.10 ±1.271	3.60 ±1.075	3.34 ±0.000	3.90 ±0.000	3.45								
6	Scotch Bere	2.30 ±0.619	2.57 ±1.373	3.10 ±0.000	2.95 ±0.000	2.90 ±0.000	2.60							
7	O.A.C. 21	2.52 ±0.394	2.01 ±0.614	2.51 ±1.593	2.55 ±0.000	2.90 ±1.633	1.42 ±0.000	1.62						
8	Golden Promise	2.50 ±0.000	3.25 ±1.135	3.10 ±0.000	3.55 ±0.000	3.15 ±1.062	2.50 ±0.000	2.43 ±1.556	3.15					
9	Maris Baldric	3.35 ±0.447	2.80 ±0.298	3.17 ±0.825	3.25 ±0.538	3.55 ±0.000	2.85 ±1.033	2.05 ±0.000	3.30 ±0.000	3.75				
10	Midas	3.40 ±0.537	3.05 ±0.000	3.90 ±0.943	3.85 ±1.372	3.65 ±0.000	2.80 ±0.934	2.30 ±1.147	3.85 ±0.000	3.65 ±0.553	3.50			
11	Mosane	3.15 ±0.734	3.25 ±1.493	3.60 ±0.636	3.05 ±0.500	2.90 ±0.472	3.00 ±0.000	2.95 ±1.222	3.31 ±0.000	3.00 ±0.000	3.25 ±0.000	4.25		
12	Sultan	4.20 ±1.220	3.80 ±1.064	4.45 ±0.000	3.00 ±0.000	3.60 ±0.000	3.35 ±1.057	2.10 ±0.000	2.30 ±0.000	3.45 ±1.592	3.40 ±0.000	3.95 ±1.213	3.90	
13	Boreham Warrior	2.35 ±0.000	3.00 ±1.640	4.10 ±1.853	3.15 ±0.000	2.87 ±1.200	2.30 ±0.601	1.65 ±0.000	3.15 ±0.000	3.30 ±0.000	3.00 ±0.654	2.90 ±0.000	4.10 ±0.958	2.30

TABLE 5-9

Productive tiller no: means and genetic standard deviations, F_2, 1971 data

		1	2	3	4	5	6	7	8	9	10	11	12	13
1	Olli	3.00												
2	Pirkka	2.79 ±1.263	2.41											
3	Cambrinus	3.75 ±0.000	3.35 ±0.395	4.40										
4	Ymer	4.05 ±1.213	3.90 ±0.916	4.50 ±0.742	4.95									
5	Deba Abed	3.60 ±1.130	3.90 ±0.247	3.95 ±1.333	4.20 ±0.000	4.05								
6	Scotch Bere	2.90 ±0.897	2.65 ±0.000	3.05 ±1.171	3.95 ±0.615	3.95 ±1.633	3.05							
7	O.A.C. 21	2.75 ±0.000	2.79 ±1.209	3.45 ±0.000	3.25 ±0.830	2.95 ±0.000	2.80 ±0.000	2.44						
8	Golden Promise	2.95 ±1.128	3.70 ±0.000	3.40 ±0.000	3.35 ±0.000	3.80 ±0.577	3.40 ±1.329	2.90 ±0.000	3.85					
9	Maris Baldric	4.70 ±0.587	3.95 ±1.085	3.65 ±0.000	4.65 ±0.000	3.95 ±0.820	3.50 ±0.000	3.75 ±0.394	4.15 ±0.000	3.85				
10	Midas	2.85 ±0.516	3.40 ±0.820	4.70 ±0.000	4.00 ±1.202	4.25 ±1.391	3.80 ±0.000	3.00 ±0.000	3.20 ±0.675	3.65 ±0.000	3.10			
11	Mosane	4.30 ±0.000	3.75 ±0.128	4.20 ±1.011	4.90 ±0.000	4.25 ±0.817	3.55 ±1.515	4.10 ±1.078	4.40 ±0.000	4.25 ±0.000	4.70 ±1.973	3.70		
12	Sultan	3.55 ±1.128	3.75 ±1.787	4.35 ±0.760	4.20 ±0.000	3.70 ±1.229	3.40 ±0.298	3.50 ±0.000	3.45 ±0.000	3.85 ±0.000	4.30 ±0.687	4.30 ±0.000	4.25	
13	Boreham Warrior	3.70 ±0.703	3.40 ±1.030	4.00 ±0.000	3.85 ±1.576	3.55 ±0.000	3.55 ±1.135	2.70 ±0.448	3.90 ±0.667	4.15 ±0.000	4.80 ±0.402	3.70 ±0.000	4.50 ±0.654	3.85

TABLE 5-10

Grains per ear: means and genetic standard deviations, F_2, 1970 data

		1	2	3	4	5	6	7	8	9	10	11	12	13
1	Olli	26.3												
2	Pirkka	±30.7 ± 7.08	31.7											
3	Cambrinus	±18.3 ± 6.22	±19.6 ± 5.18	16.2										
4	Ymer	±21.7 ± 5.96	±23.1 ± 6.32	±17.0 ± 0.00	16.2									
5	Deba Abed	±23.6 ± 6.92	±21.0 ± 7.75	±18.4 ± 0.38	±19.7 ± 0.00	19.0								
6	Scotch Bere	±32.9 ± 0.00	±32.2 ± 2.48	±19.5 ± 4.00	±23.1 ±10.25	±20.8 ± 6.03	27.4							
7	O.A.C. 21	±27.5 ± 6.49	±34.7 ± 0.00	±18.8 ± 6.57	±19.7 ± 3.28	±21.9 ± 6.89	±25.3 ± 0.00	28.0						
8	Golden Promise	±17.4 ± 2.50	±22.1 ± 6.71	±17.7 ± 0.00	±16.6 ± 1.86	±18.5 ± 1.96	±22.3 ± 7.48	±22.1 ± 7.18	16.8					
9	Maris Baldric	±22.1 ± 0.00	±19.3 ± 0.00	±19.3 ± 1.75	±17.5 ± 2.52	±23.0 ±13.26	±23.6 ± 9.07	±19.9 ± 4.00	±17.7 ± 1.64	17.7				
10	Midas	±23.7 ± 9.51	±21.2 ± 4.27	±18.8 ± 2.48	±20.0 ± 0.00	±17.8 ± 0.44	±31.0 ±12.86	±19.4 ± 6.58	±18.1 ± 0.00	±19.3 ± 0.00	20.1			
11	Mosane	±19.7 ± 2.95	±17.6 ± 0.00	±17.9 ± 0.00	±17.4 ± 2.49	±16.8 ± 0.00	±22.3 ± 8.91	±21.9 ± 6.79	±18.6 ± 2.09	±18.7 ± 2.10	±18.1 ± 1.91	16.1		
12	Sultan	±17.9 ± 1.53	±22.3 ± 9.39	±17.2 ± 3.23	±16.8 ± 0.00	±19.1 ± 0.00	±23.0 ± 7.14	±20.5 ± 6.80	±15.9 ± 0.00	±16.6 ± 1.35	±17.8 ± 0.00	±16.2 ± 1.22	14.4	
13	Boreham Warrior	±21.7 ± 6.67	±20.0 ± 2.78	±18.8 ± 2.32	±18.1 ± 0.00	±18.4 ± 1.78	±25.7 ±11.29	±21.9 ± 6.93	±18.1 ± 0.00	±20.0 ± 0.00	±17.7 ± 1.18	±18.9 ± 2.29	±18.9 ± 1.81	17.1

TABLE 5-11

Grains per ear: means and genetic standard deviations, F_2 1971 data

		1	2	3	4	5	6	7	8	9	10	11	12	13
1	Olli	38.7												
2	Pirkka	42.1 ±11.33	42.9											
3	Cambrinus	23.6 ± 8.52	23.3 ± 9.99	19.8										
4	Ymer	23.9 ± 6.30	25.8 ±13.45	21.8 ± 0.00	19.9									
5	Deba Abed	31.6 ±15.98	27.5 ±11.92	21.2 ± 0.00	22.9 ± 1.91	23.3								
6	Scotch Bere	37.6 ± 2.72	39.3 ±12.17	26.0 ± 7.86	30.7 ± 3.10	38.1 ±15.22	41.4							
7	O.A.C. 21	33.9 ± 4.79	37.9 ± 0.00	26.5 ±13.58	21.9 ±10.42	25.1 ± 8.82	45.5 ± 0.00	39.5						
8	Golden Promise	29.1 ±15.61	29.6 ±13.80	20.1 ± 2.97	20.7 ± 1.37	21.4 ± 0.00	32.3 ± 7.37	22.4 ± 5.36	20.9					
9	Maris Baldric	30.3 ±13.44	26.1 ± 7.84	22.5 ± 0.00	22.2 ± 0.00	21.8 ± 1.70	35.4 ±10.92	25.2 ± 7.33	21.3 ± 1.56	20.2				
10	Midas	24.8 ± 6.48	32.3 ±14.50	22.7 ± 3.58	23.8 ± 0.00	24.1 ± 2.39	34.6 ± 9.54	28.5 ±12.65	23.4 ± 0.00	22.5 ± 2.62	22.9			
11	Mosane	27.3 ± 7.97	32.3 ±12.94	21.1 ± 0.00	22.6 ± 0.00	22.1 ± 0.97	33.9 ±13.38	27.3 ±10.27	21.5 ± 4.94	21.2 ± 0.00	23.7 ± 5.52	19.7		
12	Sultan	22.5 ± 5.46	24.2 ± 9.96	20.8 ± 2.38	21.6 ± 2.57	23.0 ± 3.67	34.1 ±16.20	23.5 ± 0.00	21.9 ± 2.73	22.6 ± 2.87	22.6 ± 0.00	22.1 ± 3.38	19.6	
13	Boreham Warrior	26.0 ±11.31	28.3 ±12.32	22.8 ± 1.47	23.4 ± 1.05	22.2 ± 1.57	34.9 ±13.86	26.0 ±12.89	23.3 ± 1.23	23.1 ± 0.00	22.6 ± 0.51	24.5 ± 4.53	22.7 ± 0.00	22.4

TABLE 5-12

1000 Corn weight: means and genetic standard deviations, F_2 1971 data

		1	2	3	4	5	6	7	8	9	10	11	12	13
1	Olli	38.2												
2	Pirkka	± 36.7 5.75	36.7											
3	Cambrinus	± 45.0 0.00	± 46.1 4.37	45.3										
4	Ymer	± 48.1 8.32	± 47.6 10.13	± 46.4 4.57	43.1									
5	Deba Abed	± 43.9 7.36	± 47.5 7.67	± 42.2 0.00	± 44.9 2.85	43.2								
6	Scotch Bere	± 36.8 0.00	± 41.8 4.57	± 37.8 9.75	± 37.3 6.50	± 39.3 6.27	40.1							
7	O.A.C. 21	± 36.1 5.54	± 37.1 0.00	± 48.9 8.63	± 48.3 4.45	± 44.7 8.87	± 36.5 0.00	36.0						
8	Golden Promise	± 43.8 6.58	± 47.1 10.26	± 40.8 4.86	± 40.6 5.49	± 45.0 2.10	± 36.5 11.64	± 46.4 0.96	34.4					
9	Maris Baldric	± 45.5 7.17	± 51.2 0.00	± 46.8 3.79	± 45.0 7.22	± 44.8 0.00	± 39.7 10.65	± 46.9 11.29	± 44.6 5.54	44.6				
10	Midas	± 46.1 5.13	± 45.6 7.28	± 42.2 3.53	± 43.4 0.00	± 44.2 0.00	± 39.4 7.77	± 45.2 6.91	± 36.2 3.87	± 45.7 6.37	35.5			
11	Mosane	± 45.7 3.35	± 48.0 8.32	± 44.7 0.00	± 43.5 0.00	± 43.5 3.92	± 37.6 9.20	± 44.0 7.73	± 44.4 0.00	± 46.4 0.00	± 42.2 4.41	41.9		
12	Sultan	± 52.7 4.73	± 48.1 7.44	± 44.6 6.35	± 46.2 4.23	± 44.1 5.35	± 39.6 7.13	± 45.8 0.00	± 44.5 3.86	± 45.5 3.32	± 47.3 0.00	± 45.4 4.98	42.1	
13	Boreham Warrior	± 51.6 10.50	± 51.4 6.20	± 50.3 5.58	± 51.3 2.04	± 46.3 2.87	± 43.6 9.16	± 46.2 10.94	± 45.8 7.43	± 51.3 0.00	± 46.1 3.19	± 51.4 2.85	± 52.2 0.00	50.5

arrangement should be used. However, information derived from the diallel analysis can be used in conjunction with these means and variances in predicting the value of various combinations from early generation trials (Hayes, 1965).

If the trait under consideration is determined almost entirely by additive effects with no dominance or non-allelic interaction then the best segregates should be found in a cross within the array of a diallel table, which has the highest expression of that trait. Ideally the individual cross within this array should have a high mean and high variance. On the other hand, where there is high dominance, uncomplicated by other genetic effects, the Wr, Vr graphs can indicate whether the top dominant or bottom recessive is present amongst the parents (Crumpacker and Allard, 1962). If it is, then the limits of selection have been reached in the population.

Dominance and, in some cases, epistasis were detected in the inheritance of the three major components of yield and dominance was always found to be acting in an increasing direction. If the breeder were to confine his attention to this particular population he should by intercrossing the best segregants (assortative mating) obtain a reassociation of the genes in such a way that an excess of combinations giving extreme expression is achieved, though at the expense of the more balanced combinations (Breese, 1956). Where dominance was absent this would

result in the fixation of extreme expression due to homozygosis of reinforcing gene combinations. Where dominance or more complex genetic control was present, reinforcing homozygous/heterozygous and heterozygous/heterozygous combinations would also be involved and the progress to fixation would be slower.

The detection of non-additive genetic effects in the components of the complex character yield indicates that heterosis for yield in barley, claimed by other workers, cannot necessarily be explained (Williams, 1959) as simply the result of a multiplicative interaction between components which are determined by an essentially additive genetic system. Williams (loc cit), though in a different context, also raised the possibility of undesirable consequences when selection for extremes of expression is practised leading to fixation above the optimal level of fitness. If too many components are simultaneously at too high a level the tolerance-level of the product of component interaction may be exceeded. If yield had reached an upper limit, it might be expected that the components of yield would be negatively correlated. The fact that this was not the case in the population under study is perhaps an indication that considerable further improvement should be possible.

The purpose of this study was to investigate the inheritance of those traits which are important in determining yield in barley. The analyses of four

traits: productive tiller number, grains per ear, 1000 corn weight, and time to heading (see attached paper) are presented. Analyses have yet to be conducted on the traits: height at harvest, degree of mildew susceptibility and grain nitrogen.

Although 6-rowed genotypes are not commonly grown commercially in Britain, they were included for the purposes of another project, to study the genetics of diastase production. The inclusion of these genotypes did, however, allow comparisons to be drawn between the two types of cultivated barley in the expression and inheritance of the major components of yield.

PART II

MULTIVARIATE STUDIES

CHAPTER 6

THE APPLICATION OF CANONICAL ANALYSIS TO DATA FROM A DIALLEL EXPERIMENT

For this analysis the data for the two blocks were pooled giving a maximum of twenty plants per family. The results were essentially similar in both seasons and the data from 1971 only are dealt with here.

Initially seven traits were included in the analysis. These were:

1) mildew score on June 22nd (% leaf cover);
2) days from May 1st to ear emergence;
3) height at harvest (cm);
4) productive tiller number;
5) number of grains per ear;
6) straw weight (g);
7) 1000 corn weight (g).

Analyses were also conducted on data for those traits for which information was already available from the diallel analyses. These were traits 2, 4, 5 and 7 as listed above. In addition, the estimate of grain yield, obtained as the product of the three yield components, was included to make a total of five traits.

Details of the analysis are given in Appendix V.

RESULTS

The 13 x 13 half diallel, F_1 - seven traits

All seven latent roots were significantly different

from zero at the 0.1% level and the proportions of the total variation accounted for by these axes were 49%, 24%, 14%, 8%, 2%, 2%, 1% respectively. Thus there was strictly no reduction in the number of dimensions on which the data could be adequately represented.

The canonical vectors which apply to the standardized values for the traits (see Chapter 7) show the weightings given to each trait in the derivation of the corresponding canonical axis. The first four canonical vectors, accounting for approximately 95% of the total variation, are shown in table 6-1.

TABLE 6-1

Canonical vectors for the standardized data for seven traits from the 13 x 13 half diallel F_1, 1971

Trait	Vector			
	1	2	3	4
1. Mildew score	-0.549	0.097	0.992	0.689
2. Days to heading	0.855	-0.099	-0.416	1.241
3. Height at harvest	-1.243	0.109	-1.182	0.656
4. Productive tiller number	0.592	0.012	0.517	0.145
5. Grains per ear	-0.031	-0.799	0.168	0.110
6. Straw weight	0.297	-0.055	-0.457	-0.408
7. 1000 corn weight	0.342	1.208	0.344	0.157
Latent roots	3.3525	1.6305	0.9405	0.5711
% total variation	48.7	23.7	13.7	8.3

Axes 1 and 2 were plotted against each other (73%

of the total variation) and the scatter diagram for the parents and the hybrids involving the 6-rowed parent Olli (1) is shown in figure 6-1. The use of scatter diagrams to illustrate the spatial arrangement of groups is obviously limited to two dimensions and can therefore be misleading. However, figure 6-1 illustrates clearly the separation of the 6-rowed parents from the 2-rowed parents, particularly on the first axis. In the derivation of this axis the heaviest weighting was given to the trait height at harvest and this trait, together with time to heading, was clearly of more significance in the discrimination of the two barley types, as represented by these particular genotypes, than was the trait grains per ear.

Hybrids between Olli and the other three 6-rowed parents fell very close to the parents on both axes, but hybrids between Olli and the 2-rowed parents were markedly displaced from both parental populations and were grouped very closely. This displacement was most marked on the second axis and inspection of table 6-1 shows that in the derivation of this axis the trait 1000 corn weight played a large part.

Such deviations of the hybrids from positions midway between the parents may be attributed to the effects of dominance and epistasis (Whitehouse, 1970 b), and would seem to confirm the previous finding (Chapter 4) that epistasis occurred in crosses between 6-rowed and 2-rowed parents for the trait 1000 corn weight. The

Figure 6-1. Parents and Olli array F_1.

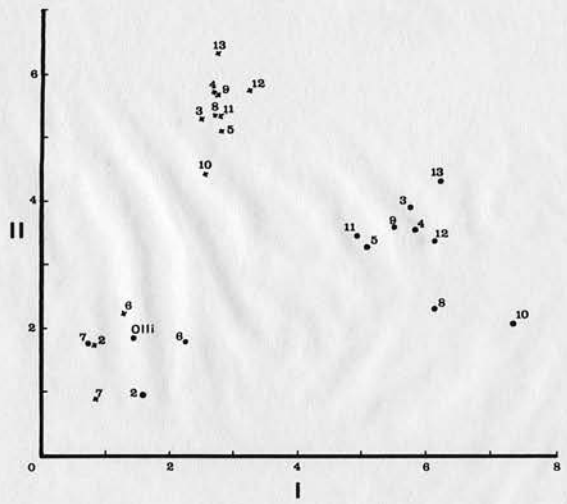


Figure 6-2. Parents and Cambrinus array F_1.

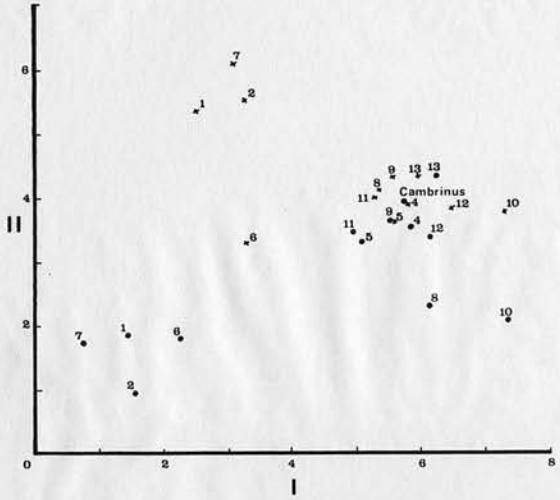


Figure 6-3. Parents and Olli array F_2.

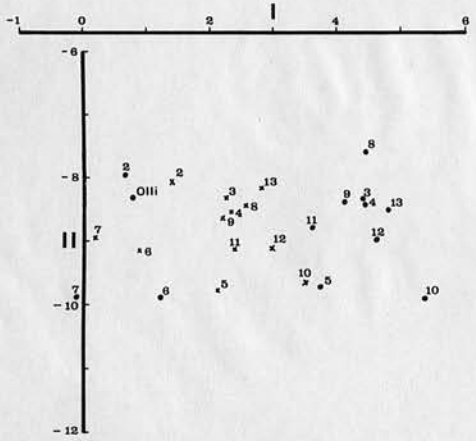
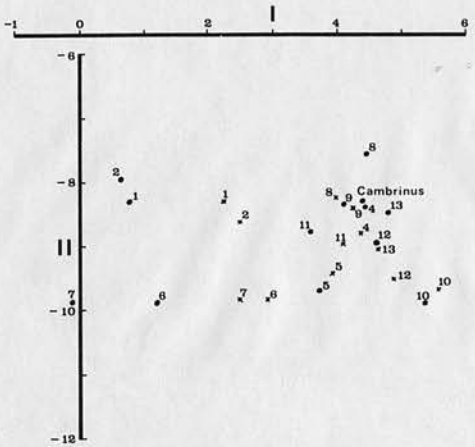


Figure 6-4. Parents and Cambrinus array F_2.



• = Parents.

x = Hybrids between recurrent parent and the parent numbered.

deviations from the mid-parental position on the first axis were not so marked but again suggested that non-additive genetic effects were present in the traits chiefly involved in the derivation of this axis. Information for the trait height at harvest was not available but it was shown (Riggs and Hayter, 1972) that partial dominance was operative in the inheritance of time to heading.

When the hybrids of a 2-rowed parent, e.g. Cambrinus (3) were plotted, a very similar situation was observed (figure 6-2). However, an obvious exception was the hybrid between Cambrinus and Scotch Bere (6) which fell close to the mid-parental position on both axes. When the co-ordinates for the hybrids between Scotch Bere and the other 2-rowed parents were plotted these too fell close to the mid-parental position. It was remarked in Chapter 4 (figure 4-12) that Scotch Bere did not behave as the other 6-rowed genotypes for the trait 1000 corn weight and it would appear from figure 6-2 that the interaction between 2-rowed and 6-rowed genotypes for this trait did not involve Scotch Bere.

The 13 x 13 half diallel, F_2 - seven traits

The analysis was conducted on the F_2 data using the same traits and again seven latent roots were significantly greater than zero and the respective axes accounted for 53%, 18%, 12%, 8%, 4%, 3%, 2% of the total variation. The first two axes are plotted for the parents and the

Olli array in figure 6-3 and for the parents and the Cambrinus array in figure 6-4. The canonical vectors corresponding to the standardized data are given in table 6-2 and show that the heaviest weighting was given to the trait height at harvest for the first axis and also for the second axis with slightly lower weightings given to mildew score and days to heading. The influence of non-additive genetic effects was much lower in this generation and most of the points representing hybrids fell close to a mid-parental position on the two axes.

TABLE 6-2

Canonical vectors for the standardized data for seven traits from the 13 x 13 half diallel F_2, 1971

Trait	Vector			
	1	2	3	4
1. Mildew score	-0.492	0.771	0.765	-0.064
2. Days to heading	0.617	-0.677	1.038	-0.001
3. Height at harvest	-1.057	-0.955	0.304	0.596
4. Productive tiller number	0.588	0.389	0.315	-0.116
5. Grains per ear	-0.049	-0.046	0.167	-0.552
6. Straw weight	0.098	-0.386	-0.439	-0.043
7. 1000 corn weight	0.543	0.492	0.175	0.707
Latent roots	1.8339	0.6011	0.4113	0.2794
% total variation	53.6	17.6	12.0	8.2

TABLE 6-3

Between-parent distances derived from canonical analysis of seven traits for the F_2 diallel, 1971

		1	2	3	4	5	6	7	8	9	10	11	12
1.	Olli												
2.	Pirkka	2.61											
3.	Cambrinus	3.90	4.37										
4.	Ymer	4.20	4.33	1.14									
5.	Deba Abed	3.48	4.36	1.61	2.05								
6.	Scotch Bere	3.09	2.43	3.99	3.76	3.32							
7.	O.A.C. 21	2.90	2.85	4.91	4.82	4.15	1.68						
8.	Golden Promise	4.30	4.20	1.75	1.78	2.91	4.43	5.31					
9.	Maris Baldric	4.02	3.96	1.06	0.90	2.01	3.48	4.49	1.61				
10.	Midas	5.05	5.43	2.27	2.60	2.20	4.69	5.73	2.68	2.56			
11.	Mosane	3.38	3.83	1.05	1.40	1.24	3.18	3.97	2.04	1.01	2.48		
12.	Sultan	4.33	4.56	1.18	0.75	1.72	3.75	4.83	2.01	1.04	2.03	1.32	
13.	Boreham Warrior	5.06	4.60	2.02	1.66	2.86	3.94	5.23	2.57	1.43	2.98	2.26	1.66

The distance between two points on the canonical axes is the square root of the sum of squares of the difference on each axis. Distances between parents, as determined from the analysis of the F_2 generation and parents, are shown in table 6-3. The progeny of crosses made between parents such as Ymer (4), Maris Baldric (9), and Sultan (12), which were closely grouped by the analysis, would be unlikely, on this evidence alone, to be very much different from their parents with respect to the traits measured. On the other hand, promising segregants might be found amongst the progeny of crosses between 2-rowed parents, placed farther apart, such as Golden Promise (8) and Deba Abed (5), Deba Abed and Boreham Warrior (13), Boreham Warrior and Midas (10). Such segregants might combine the best phenotypic performance of both parents and would therefore represent positive plant breeding gains.

The 13 x 13 half diallel - five traits

The number of traits involved in the analysis was reduced by considering only the components of yield, yield itself as the product of these components, and days to heading. Figure 6-5 shows the points for the parents and for the Olli array at F_1 plotted on the first two axes which accounted for 86.5% of the total variation. Again the trait 1000 corn weight was given heavy weighting in determining the discrimination on the second axis (table 6-4) and the progeny of Olli and the 2-rowed

Figure 6-5. Parents and Olli array F_1 .

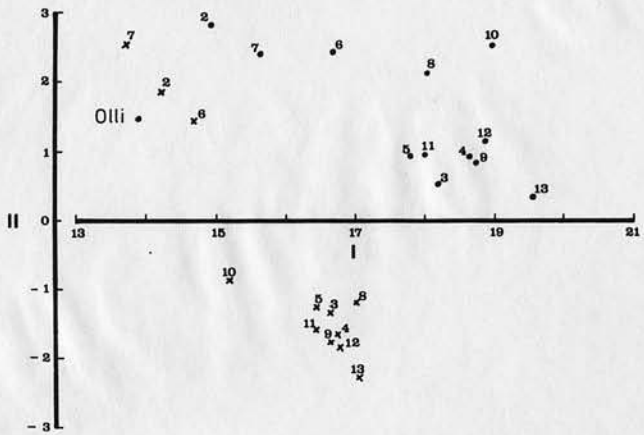


Figure 6-6. Parents and Cambrinus array F_1 .

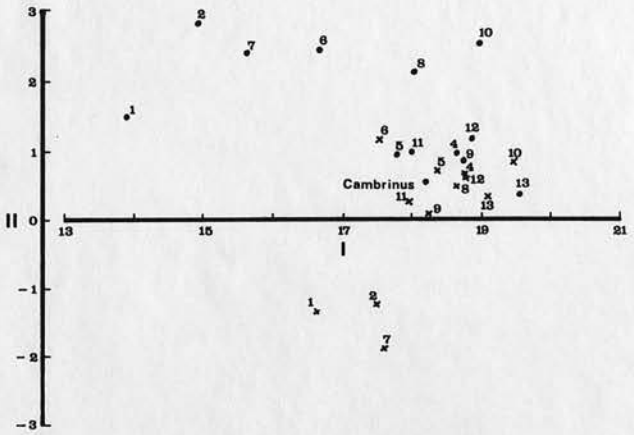


Figure 6-7. Parents and Olli array F_2 .

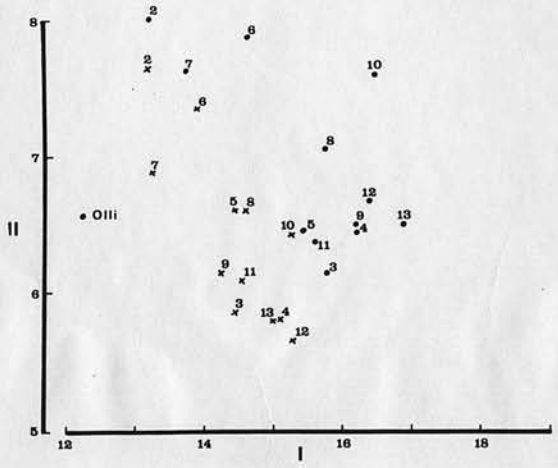
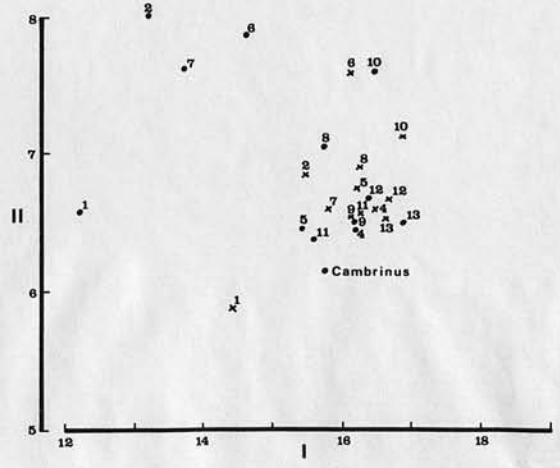


Figure 6-8. Parents and Cambrinus array F_2 .



parents were markedly displaced from the mid-parental position.

TABLE 6-4

Canonical vectors for the standardized data for five traits from the 13 x 13 half diallel F_1, 1971

Trait	Vector 1	2	3	4	5
1. Productive tiller number	0.355	-0.361	-1.293	1.013	3.129
2. Grains per ear	-0.563	0.361	0.192	1.046	2.263
3. 1000 corn weight	0.270	-1.362	0.381	0.626	1.242
4. Yield	0.152	0.568	1.201	-2.257	-3.250
5. Days to heading	1.376	0.525	0.469	0.277	0.145
Latent roots	1.8331	1.6947	0.2823	0.1652	0.1012
% total variation	45.0	41.6	6.9	4.0	2.5

The graph showing the positions of the points representing the Cambrinus array at F_1 (figure 6-6) depicts a situation similar to that in figure 6-2, and again no interaction was evident for the cross between Cambrinus and the 6-rowed Scotch Bere.

In the F_2 generation (figures 6-7 and 6-8), the trait days to heading was given the heaviest weighting in the first axis and the traits grains per ear and days to heading were of most importance in determining the discrimination on the second axis (table 6-5). These

two axes accounted for 81.9% of the total variation. Little evidence of non-additive effects was apparent from the graphs.

TABLE 6-5

Canonical vectors for the standardized data for five traits from the 13 x 13 half diallel F_2, 1971

Trait	Vector 1	2	3	4
1. Productive tiller number	0.453	0.073	-0.456	-1.035
2. Grains per ear	-0.388	0.814	0.542	-0.404
3. 1000 corn weight	0.202	-0.531	0.844	-0.017
4. Yield	-0.017	-0.109	0.356	0.082
5. Days to heading	1.195	0.611	0.283	0.066
Latent roots	1.0963	0.3448	0.1916	0.0750
% total variation	62.3	19.6	10.9	4.3

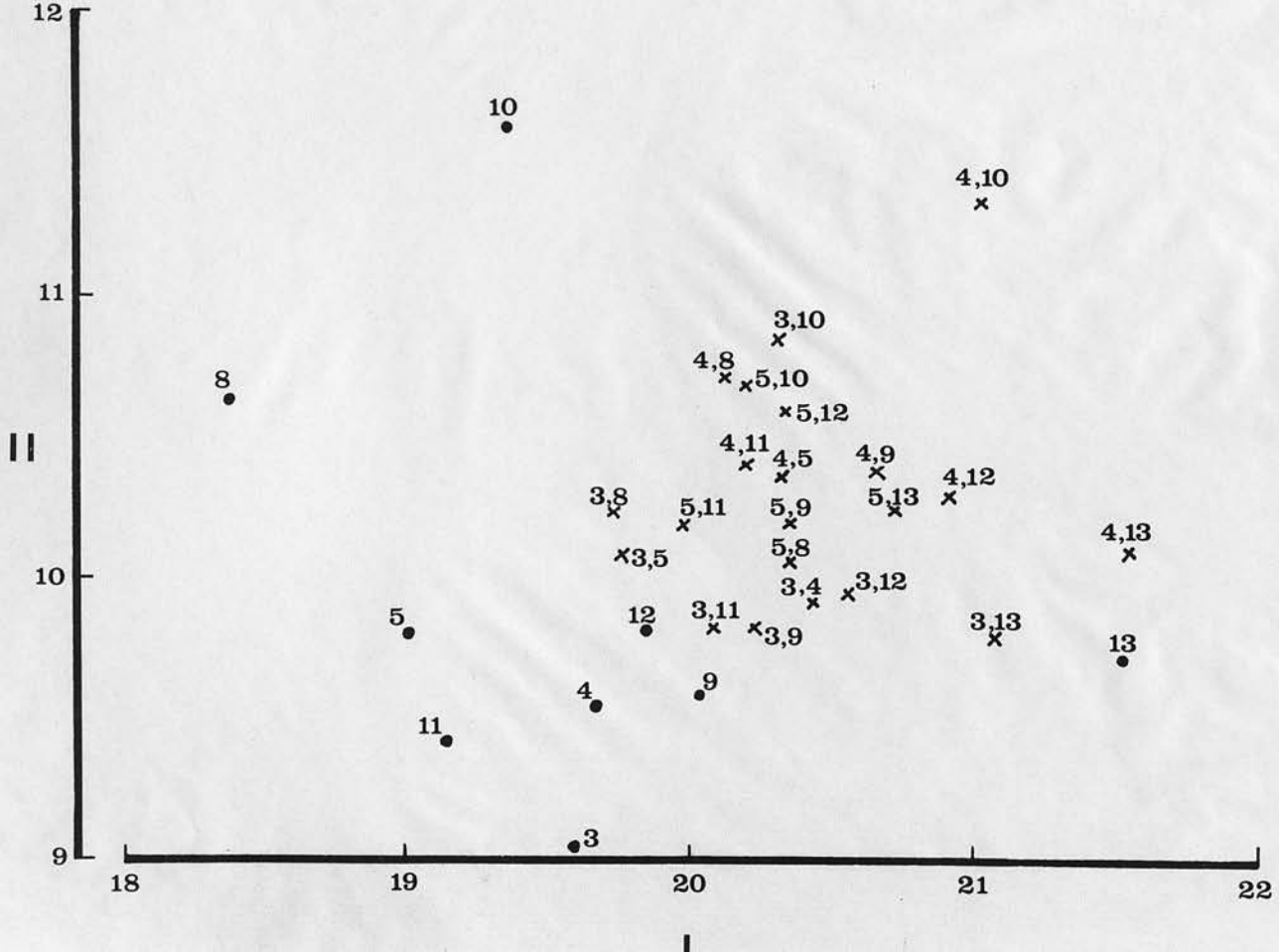
The 9 x 9 F_2 half diallel of 2-rowed genotypes - five traits

Only two of the latent roots were significantly greater than zero so that the scatter diagram in figure 6-9 represents the total significant discrimination between families. The hybrid arrays of Cambrinus, Ymer and Deba Abed only were plotted so as not to crowd the diagram.

The distances between the parents are given in table 6-6 and are of considerable interest since they show the similarities and differences between the parents with

9 x 9 DIALLEL OF 2-ROWED GENOTYPES 1971.

Figure 6-9. 2-rowed parents and arrays of Cambrinus (3), Ymer (4) and Deba Abed (5), F_2, 5 traits.



respect to the five important traits analysed. The varieties Ymer, Maris Baldric and Sultan were very closely grouped, as in table 6-3, whilst Boreham Warrior, Midas and Golden Promise were markedly distinct. Similarities between certain parents were not entirely unexpected since several of the varieties have been developed by selection for the same or similar criteria of phenotypic performance. Some have common ancestors in their pedigrees (table 3-1). Thus Cambrinus, Mosane and Sultan all have Balder in their parentage. On the other hand Maris Baldric and Boreham Warrior have similar pedigrees but do not much resemble each other.

TABLE 6-6

Distances, between 2-rowed parents, derived from canonical analysis of five traits for the F_2 diallel, 1971

	3	4	5	8	9	10	11	12
3. Cambrinus								
4. Ymer	0.50							
5. Deba Abed	0.97	0.72						
8. Golden Promise	2.01	1.70	1.04					
9. Maris Baldric	0.71	0.38	1.06	1.96				
10. Midas	2.56	2.08	1.81	1.37	2.11			
11. Mosane	0.58	0.54	0.43	1.45	0.92	2.20		
12. Sultan	0.81	0.33	0.84	1.68	0.30	1.84	0.82	
13. Boreham Warrior	2.04	1.86	2.52	3.28	1.49	2.86	2.40	1.68

In the absence of epistasis the prospects for improvements over the parents are likely to be greater in the progenies of parents placed rather far apart in such an analysis than in the progenies of parents such as Maris Baldric and Sultan which are virtually indistinguishable.

The deviations of the hybrids from the mid-parental position on both axes in figure 6-9 suggests that non-additive effects were operative in one or more of those traits which were given heavy weightings in the derivation of these axes. Table 6-7 shows that these traits were 1000 corn weight and days to heading. Whilst complete dominance was found in F_1 for 1000 corn weight in the 2-rowed genotypes (Chapter 4), dominance was low or absent for the trait days to heading in this population (Riggs and Hayter, 1972) so that dominance, but probably not interaction, associated with the trait 1000 corn weight was still apparent at F_2.

TABLE 6-7

Canonical vectors for the standardized data for five traits from the 2-rowed genotypes F_2, 1971

	1	2
1. Productive tiller number	-0.028	-0.227
2. Grains per ear	-0.263	0.654
3. 1000 corn weight	0.972	-0.900
4. Yield	0.296	0.357
5. Days to heading	0.890	0.669
Latent roots	0.5084	0.3196
% total variation	51.2	32.2

DISCUSSION

These analyses confirmed, though perhaps with less objectivity, several of the findings from the biometrical analyses described in Part I of this thesis.

Whitehouse (1970 b) concluded, from an analysis of data from a barley diallel experiment, that deviations of the hybrid positions from the mid-parental positions were sufficiently small and consistent, at around 35% of the parental distance, for the hybrid position to be predicted. The closeness of these predicted positions to the breeder's targets could then be assessed (see Chapter 2). In the present data the greatest degree of apparent additivity, when comparing the positions of the hybrids with those of their parents, was generally on the first axis and one might expect that the traits most heavily weighted in the derivation of this axis would be determined very largely by additive genetic effects. Non-additive effects were usually very apparent in the second axis, which, in one case, contained 41.6% of the total variation, in the F_1 analyses. Even in the F_2 generation deviations of the hybrid position from the mid-parent position could, in some cases, be quite large (tables 6-8 and 6-9).

Prediction of hybrid positions as suggested by Whitehouse (*loc cit*) would probably not be very precise in generations earlier than F_3, at least for the traits involved in this analysis. It should be safer to aim for a region of space as the breeding target rather than for a point, and an illustration of this as a method of

TABLE 6-8

Distances derived from canonical analysis of seven traits, 1971 diallel

		F_1 analysis		F_2 analysis	
		Distance between Olli and P_n	Deviation of hybrid from mid-point	Distance between Olli and P_n	Deviation of hybrid from mid-point
1.	Olli	-	-	-	-
2.	Pirkka	3.04	1.07	2.61	1.09
3.	Cambrinus	4.98	2.87	3.90	1.10
4.	Ymer	5.18	3.22	4.20	1.75
5.	Deba Abed	4.36	2.76	3.48	1.17
6.	Scotch Bere	3.56	0.82	3.09	0.81
7.	O.A.C. 21	3.31	1.56	2.90	0.84
8.	Golden Promise	5.32	3.77	4.30	1.32
9.	Maris Baldric	5.09	3.11	4.02	1.09
10.	Midas	6.28	3.37	5.05	1.56
11.	Mosane	4.34	2.85	3.38	1.13
12.	Sultan	5.38	3.35	4.33	1.81
13.	Boreham Warrior	6.32	3.43	5.06	1.10

TABLE 6-9

Distances derived from canonical analysis of five traits, 1971 diallel

	F_1 analysis		F_2 analysis	
	Distance between Cambrinus and P_n	Deviation of hybrid from mid-point	Distance between Cambrinus and P_n	Deviation of hybrid from mid-point
1. Olli	4.45	2.44	3.57	0.68
2. Pirkka	4.42	3.13	3.31	1.08
3. Cambrinus	-	-	-	-
4. Ymer	0.86	0.76	0.69	0.81
5. Deba Abed	0.64	0.56	0.45	0.79
6. Scotch Bere	3.11	0.94	2.29	1.26
7. O.A.C. 21	3.48	3.48	2.59	1.36
8. Golden Promise	1.75	1.33	1.29	0.83
9. Maris Baldric	0.74	0.80	0.62	0.59
10. Midas	2.34	2.08	1.78	1.05
11. Mosane	0.64	1.00	0.50	0.77
12. Sultan	1.04	0.56	0.83	0.82
13. Boreham Warrior	1.94	0.54	1.67	0.54

selection is given in the next chapter.

The assumption that the between-line component of variance contained no non-additive genetic component was made by Eaves and Brumpton (1972) who derived narrow-sense heritability estimates for each of the canonical variates obtained in their analysis of measurements made on eighty-two F_8 lines of Nicotiana rustica. These authors also obtained, again on the assumption of no non-additivity, values for the number of effective factors associated with each canonical variate.

The arrangement of the points representing the parents in the scatter diagrams, and the estimation of distances between parents, was perhaps the most interesting information obtained from these analyses. The close grouping of Ymer, Maris Baldric and Sultan for instance (tables 6-3 and 6-6), shows that even when as many as seven traits are involved, different varieties may be scarcely distinguishable in overall performance.

Golden Promise and Midas, which are particularly short-strawed, and erect were very easily distinguished in this population, but with the arrival, and apparent success, of other short-strawed varieties, such as Maris Mink and Universe, a new stereotype for commercial barleys in the U.K. and possibly in Europe, may soon be established.

CHAPTER 7

THE USE OF CANONICAL ANALYSIS FOR SELECTION WITHIN A POPULATION OF SPRING BARLEY

The barley composite bulk populations

In setting up the barley composite bulk populations at Pentlandfield, the original stocks used as females were hybrids from the Plant Breeding Institute, Cambridge:

Hybrid	Pedigree
HB 667	Maris Baldric x Cambrinus
HB 668	Maris Baldric x Europa
HB 671	Maris Concord x Cambrinus
HB 672	Maris Concord x Europa

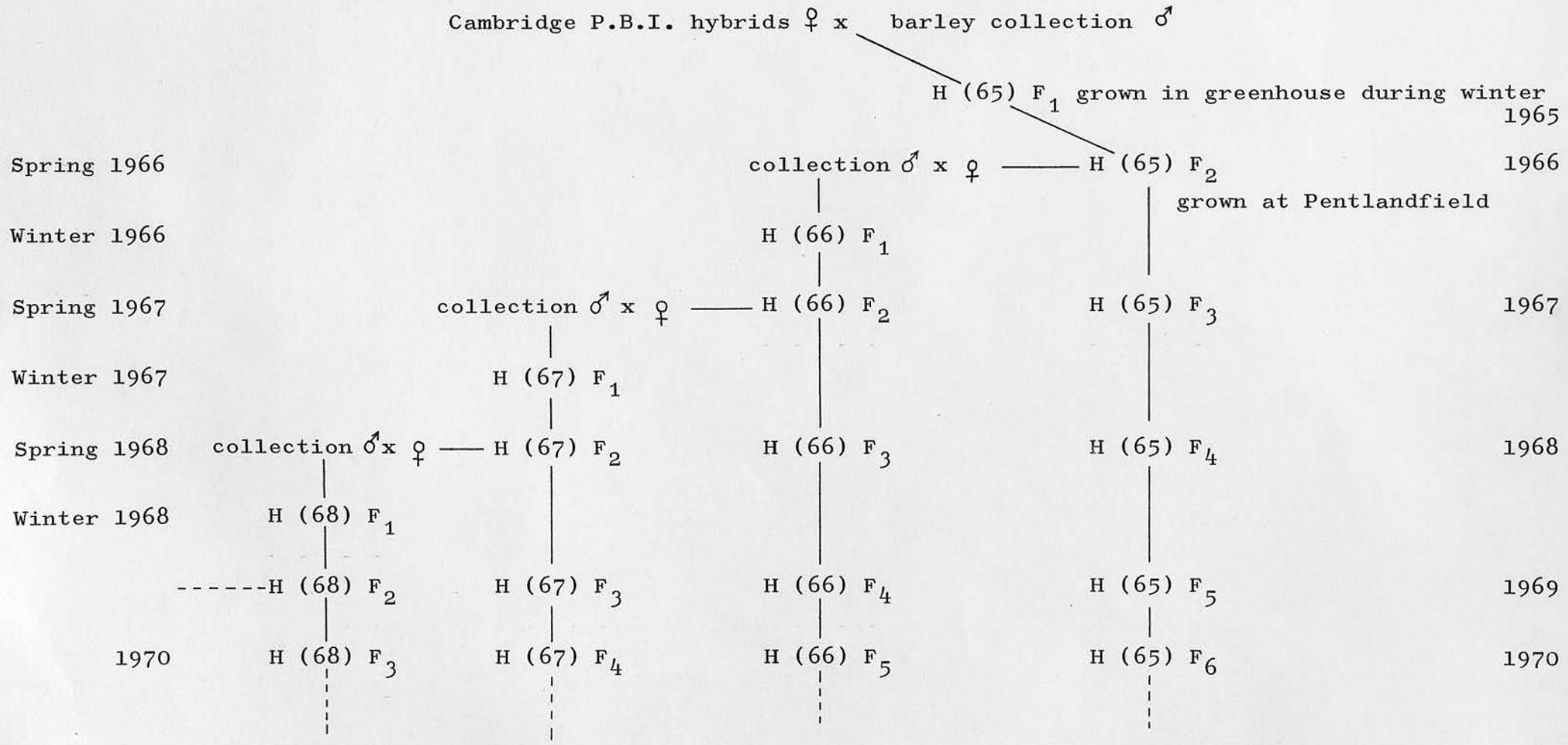
The scheme for compositing was as follows:

Plants from these crosses were emasculated and exposed in the glasshouse to pollen from plants representing a portion of the barley museum collection at Pentlandfield.

The F_1 hybrid grain was grown in the glasshouse the following winter and the F_2 seed so produced grown in the field during the summer of the next year. A portion of the F_2 was grown again in the glasshouse as intended females for a further cycle of crossing. The scheme is shown diagramatically in figure 7-1.

All F_2 generations were grown at Pentlandfield, and subsequent generations were grown at three sites respectively in the north, west and south of Scotland, each

FIGURE 7-1


Cambridge P.B.I. hybrids ♀ x barley collection ♂
H (65) F1 grown in greenhouse during winter 1965
Spring 1966
collection ♂ x ♀
H (65) F2
1966
grown at Pentlandfield
Winter 1966
H (66) F1
Spring 1967
collection ♂ x ♀
H (66) F2
H (65) F3
1967
Winter 1967
H (67) F1
Spring 1968
collection ♂x ♀
H (67) F2
H (66) F3
H (65) F4
1968
Winter 1968
H (68) F1
H (68) F2
H (67) F3
H (66) F4
H (65) F5
1969
1970
H (68) F3
H (67) F4
H (66) F5
H (65) F6
1970

population being grown at the same site each year.

Experimental material

In 1969, 1020 ear selections at F_5 were taken from a composite bulk population grown near Dunbar in East Lothian. Selection was more or less at random, the only criterion being reasonable productivity. 120 of these selections were grown in the glasshouse during the winter as ear-rows. Of these, sixty-nine produced sufficient seed to sow a replicated trial in the spring of 1970.

Each plot consisted of two rows, 16.5 cm apart and 1.22 m long with approximately twenty grains sown per row. The selections were replicated four times and six standard cultivars (Hassan, Ymer, Golden Promise, Sultan, Midas, Zephyr), eight times. The remaining 900 ear selections were sown as unreplicated ear-rows under the same conditions as the replicated trial (figure 7-2).

All the material was sown on May 6th, 1970 with a basic nitrogen fertilizer dressing of 7.5 g m^{-2}. Observations were taken for the following traits:

1) habit at seven weeks (grade 1-5, erect - prostrate);
2) days from May 30th to 50% ear emergence;
3) height at harvest in cm (mean of three measurements);
4) subjective assessment of density of tillers in the row (grade 1-5, scanty - dense);
5) mildew score on July 8th (% leaf cover according to the M.A.F.F. Guide for the Assessment of Cereal Diseases, Anon. (1971));
6) grain yield (mean yield (g) of a 1.22 m row);
7) flag leaf length (subjective grade, 1-5).

Where a subjective grade was used the material was assessed independently by two observers and the average of the two scores used.

The same plot size was used in 1971 when seventy-two composite selections were grown with four replications. The same six standards were grown with eight replications and an additional set of eight standards (Julia, Berac, Cambrinus, Wing, Vada, Gerkra, Deba Abed, Akka) with four replications. The trial was sown on April 2nd, 1971 with a basic nitrogen fertilizer dressing of 3.8 g m^{-2} and a further dressing of 3.8 g m^{-2} N was applied six weeks later.

Eight traits were recorded:

1) days from May 1st to 50% ear emergence;
2) height at harvest (cm);
3) number of heads in 30.5 cm of row (mean of two counts);
4) mildew score on June 14th (%leaf cover);
5) grain yield (g) of two 1.22 m rows;
6) grains per ear (mean of four counts);
7) ratio of grain and straw weight;
8) thousand corn weight (g).

The material was harvested by hand in both seasons. In the second season the grain:straw ratio was calculated after subtracting the grain weight from the sheaf weight to obtain the straw weight.

In the first season growing conditions were generally rather poor. High winds and light rain in mid-August led

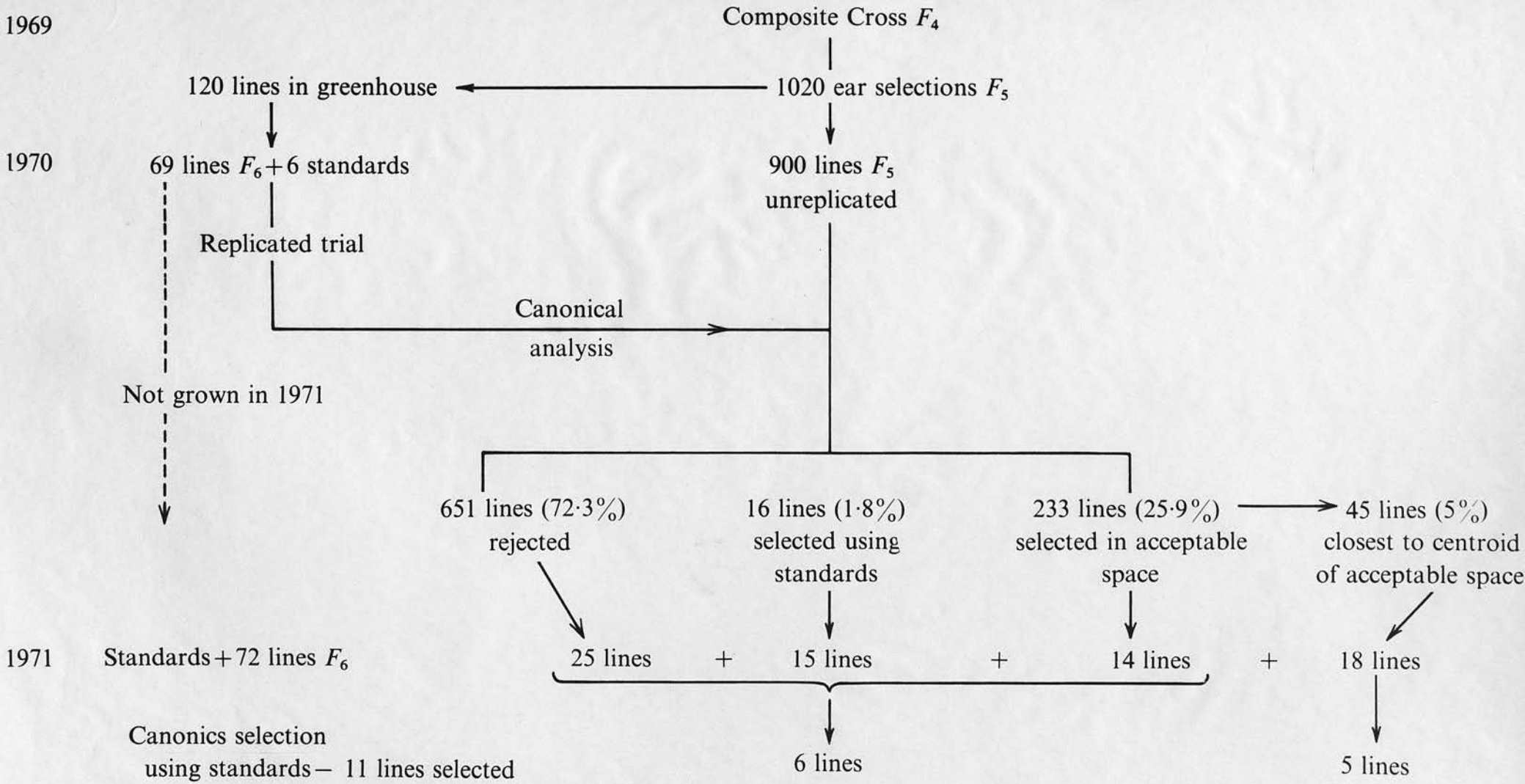

1969
Composite Cross F_4
120 lines in greenhouse
1020 ear selections F_5
1970
69 lines F_6 + 6 standards
900 lines F_5
unreplicated
Replicated trial
Canonical
analysis
Not grown in 1971
651 lines (72·3%)
rejected
16 lines (1·8%)
selected using
standards
233 lines (25·9%)
selected in acceptable
space
45 lines (5%)
closest to centroid
of acceptable space
1971
Standards + 72 lines F_6
25 lines
+
15 lines
+
14 lines
+
18 lines
Canonics selection
using standards — 11 lines selected
6 lines
5 lines

Figure 7-2

to rather severe leaning and lodging, and damp conditions prevailed during ripening. Conditions were considerably better in the second season and, although wet weather during August caused some lodging, this was not serious.

Analysis of the data was done using the I.C.L. System 4-75 computer at the Edinburgh Regional Computer Centre. The program was developed by Mr. J. L. Fyfe.

Two yield trials were grown in 1972. The larger of these was a 7 x 7 lattice square with four replications in which each plot consisted of eight rows, 16.5 cm apart and 1.5 m long. The plots were separated by a gap of 10 cm. The trial was sown on April 13th with a basic fertilizer dressing corresponding to 3.8 g m^{-2} N, and a further 3.8 g m^{-2} N were applied as a top-dressing on June 15th. Observations made during growth were tiller counts, time to ear emergence, and height. The two outside rows of each plot were discarded before harvest.

The second trial was a randomized block design with three replications. Each plot consisted of two rows 16.5 cm apart and 1.5 cm long. Border rows of spring wheat were grown between plots to reduce edge effects. This trial was sown on the same date and had the same fertilizer treatment as the larger trial.

RESULTS

Season 1970

Canonical analysis was performed on the 1970 data and five axes, accounting for 96.1% of the total

variation were found to be significant. Of these the first two axes accounted for 77.2% of the variation. The mean values and standard errors for the seven traits measured on the six standards are shown in table 7-1.

The canonical vectors obtained from the analysis of the replicated trial were used to multiply the data matrix from the unreplicated ear-rows to obtain the canonical variates. From these it was possible to assess the positions, relative to the standards, occupied by the unreplicated composite lines. The range for each canonical variate spanned by the six named standards was defined (table 7-2) and lines were looked for which had values within each of these ranges. A simple computer program was written to perform this task. Sixteen (1.8%) of the 900 lines were selected.

A slightly different approach to selection was next investigated. This involved defining acceptable upper and lower values for each of the seven traits. For this it was necessary to make decisions as to the importance of each trait in determining an "ideal" type. Where it was felt that a trait had no economic significance, no restriction on the range was imposed.

The upper and lower limits for each trait are given in table 7-3. Traits 1 and 7 (plant habit and flag leaf length) were not considered to be important criteria for the determination of an ideal type. The limits for days to ear emergence represent one day earlier and three days later than Golden Promise. Golden Promise was again

TABLE 7-1

Mean values for seven traits measured on six standards grown in 1970

Standard	Trait*						
	1 Habit	2 Days	3 Height	4 Tillers	5 Mildew	6 Yield	7 Flag leaf
1. Hassan	3.25	39.87	89.62	4.06	1.15	56.50	3.50
2. Ymer	2.37	42.25	98.50	3.31	3.22	41.87	3.00
3. Golden Promise	1.12	41.37	78.62	3.75	3.90	26.93	3.25
4. Sultan	2.62	42.62	99.75	3.81	0.62	48.50	3.00
5. Midas	1.12	45.62	79.87	3.69	1.50	40.18	3.25
6. Zephyr	2.37	39.50	109.50	3.56	2.20	45.68	3.12
S.E.	±0.20	± 0.77	± 3.38	±0.24	±0.86	± 4.24	±0.29

* For full key to traits see text

TABLE 7-2

Values for five significant canonical variates* for six standards, from the analysis of sixty-nine lines and six standards grown in 1970

Standard	Canonical variate				
	1	2	3	4	5
1. Hassan	21.117	1.152	1.518	5.043	4.615
2. Ymer	21.467	0.891	-0.811	5.322	3.529
3. Golden Promise	20.199	4.051	-1.096	5.565	2.241
4. Sultan	21.956	1.223	-0.035	4.434	3.802
5. Midas	22.579	4.689	-1.179	5.065	3.724
6. Zephyr	20.315	-0.062	-0.903	4.727	3.534
Latent roots	9.8423	1.9168	1.2540	0.9175	0.7071

* Extreme values of the range are underlined.

TABLE 7-3

Upper and lower values defined for each trait to select acceptable lines, season 1970

	Trait						
	1	2	3	4	5	6	7
	Habit	Days	Height	Tillers	Mildew	Yield	Flag leaf
Upper	5.0	44.0	93.5	5.0	2.1	99.6	5.0
Lower	1.0	40.0	78.7	4.0	0.4	70.0	1.0

TABLE 7-4

Range for five canonical variates to define acceptable space, season 1970

	Canonical variate				
	1	2	3	4	5
Upper	24.939	6.266	5.346	7.432	10.352
Lower	19.768	-1.883	-3.472	2.513	4.397

the standard for the lower limit of height and the upper limit was 5 cm shorter than Ymer. Tiller density was given narrow limits. Complete resistance to mildew was not wanted and a lower limit of 0.4% was given. The upper limit of 2.1% was the mean value of the standards. The upper limit for yield was the yield of the highest yielding of the 900 composite lines. The lower limit was higher than the yield of any of the standards. The corresponding upper and lower limits for the canonical variates were derived (table 7-4) and the 900 composite lines were again screened to select those which fell within the acceptable space.

Comparison of tables 7-2 and 7-4 shows that the range for canonical variates in the latter was wider than that in the former and indeed, using the limits of table 7-4, 233 lines were selected compared with sixteen lines when the limits of table 7-3 were used.

The vector of canonical variates corresponding to the centroid of the acceptable space was determined and D^2 (Rao, 1952: Seal, 1964) was calculated for each of these 233 lines. Selection pressure could thus be increased by selecting those lines which fell nearest to the centroid of the acceptable space.

In this way forty-five lines were selected and these did not include any of the sixteen lines selected as within the space defined by the standards, though two of these lines were also in the acceptable space. Indeed, all the lines falling within the space defined by the

standards gave yields of less than 56g which was the yield of the highest yielding standard, Hassan. Table 7-5 shows the trait means and standard deviations for the base population and the selected populations.

The data from the replicated trial were raw scores or measurements. For the purpose of grouping the lines this was quite acceptable but from the point of view of interpretation, non-standardized variables lead to difficulties because the weight of a variable varies inversely with its total standard deviation (Hope, 1968). The canonical vectors which apply to the standardized scores may be obtained by multiplying each element of vector $\underline{l}_i$ (see Appendix V) by the total standard deviation of the appropriate trait. The total standard deviation of a trait is found by taking the square root of the total sum of squares divided by the number of individuals measured.

The canonical vectors which apply to the standardized scores for traits measured in the first season are given in table 7-6. The relative magnitude of each element in a canonical vector is a direct indication of the weighting applied to each standardized trait. This is because each co-ordinate on a canonical axis was obtained by multiplying the row-vector of measurements for each barley line by the respective canonical vector (Appendix V).

From table 7-6 it can be seen that for the derivation of the first axis, considerable weighting was given to ear emergence and very low weighting to height. For the

TABLE 7-5

Means and standard deviations for seven traits in a base population of 900 lines and in three selected sub-populations grown in 1970

Population	Trait						
	1	2	3	4	5	6	7
	Habit	Days	Height	Tillers	Mildew	Yield	Flag leaf
Base population of 900 lines.	2.48 ±0.70	41.01 ± 5.92	101.39 ± 11.80	3.07 ±0.72	3.74 ±2.62	47.27 ±18.47	3.26 ±0.93
Sixteen lines within space defined by standards.	2.62 ±0.50	42.81 ± 0.98	94.63 ± 6.82	3.16 ±0.54	2.15 ±0.77	39.03 ± 9.45	2.94 ±0.68
233 lines within spaced defined by acceptable range.	2.64 ±0.55	41.76 ± 3.24	105.67 ± 8.74	3.47 ±0.57	2.95 ±1.95	64.65 ±12.86	3.29 ±0.85
Forty-five lines closest to centroid of acceptable space.	2.64 ±0.48	41.71 ± 2.40	103.64 ± 6.06	3.87 ±0.49	2.03 ±1.22	71.80 ±11.87	3.69 ±0.82

TABLE 7-6

Canonical vectors applying to the standardized scores for traits measured in 1970

Trait	Canonical vectors				
	1	2	3	4	5
growth habit	0.3561	-0.8893	1.0888	0.1493	-0.1325
days to ear emergence	2.7550	0.9910	-0.2388	0.4004	0.2268
height	0.0064	-0.9316	-0.5508	-0.1474	-0.1704
tiller density	-0.1094	0.7696	0.3918	-0.0838	-0.4347
mildew score	-0.1799	-0.1851	-0.3984	1.0670	0.1199
grain yield	0.2548	-0.0714	-0.1494	0.0784	1.4488
flag leaf length	0.1945	0.2220	0.4288	0.6740	0.2860
% total variation	64.59	12.58	8.23	6.02	4.64

second axis approximately equal weighting was given respectively to growth habit, ear emergence and height.

The scatter diagram of the first two canonical axes, plotted one against the other (figure 7-3) shows a distinct separation of the points representing the standards Midas and Golden Promise from all the other points with respect to the second axis. The remaining standards were fairly closely grouped. The scatter of points representing the composite lines overlapped the standards.

The closeness of the points for Midas and Golden Promise to each other and their separation from those for the other standards on the second canonical axis can be explained by the erect habit and short stature of these varieties as compared with the other standards (table 7-1). Both traits, as mentioned above, were given fairly heavy weighting in the derivation of the second axis (table 7-6).

Season 1971

Fifteen of the sixteen composite lines selected as falling within the space defined by the standards in 1970 were grown in 1971. Also included were thirty-two lines which had been selected as within the acceptable space, eighteen of which were among the forty-five nearest the centroid. A further twenty-five unselected lines were grown and eight additional standard varieties were included (figure 7-2 and table 7-7).

In the analysis, seven canonical axes were found to

TABLE 7-7

Mean values for eight traits measured on fourteen standards in season 1971

Standard	Trait*							
	1 Days	2 Height	3 Heads	4 Mildew	5 Yield	6 Grains/ ear	7 Grain: straw	8 1000 corn wt.
1. Hassan	54.25	87.19	48.37	3.30	173.79	21.36	0.868	44.12
2. Ymer	57.00	99.37	49.69	8.77	210.12	24.50	0.746	42.06
3. Golden Promise	55.37	74.62	46.69	13.37	155.55	23.80	0.874	35.94
4. Sultan	56.00	93.81	54.12	4.35	205.70	22.82	0.836	41.27
5. Midas	61.12	86.06	54.51	3.75	210.42	24.66	0.812	36.36
6. Zephyr	54.87	94.56	49.06	5.02	232.05	24.65	0.844	42.09
7. Julia	56.00	88.12	49.87	1.60	224.35	20.70	0.885	43.85
8. Berac	51.75	86.62	53.12	4.30	204.45	21.72	0.902	39.92
9. Cambrinus	54.50	94.37	41.00	4.50	179.92	22.97	0.781	44.72
10. Vada	53.75	96.75	54.75	2.15	271.00	23.70	1.218	47.10
11. Gerkra	54.75	99.37	50.00	1.45	214.67	24.27	0.850	43.12
12. Wing	56.50	96.50	52.50	0.60	220.05	22.90	0.831	39.80
13. Deba Abed	58.00	92.50	55.12	4.70	256.15	24.70	0.927	43.15
14. Akka	44.00	99.62	51.62	0.20	192.32	22.95	0.663	48.62
S.E. Standards 1-6	±0.45	±2.34	±3.27	±0.95	±13.73	±1.05	±0.056	±0.50
S.E. Standards 7-14	±0.64	±3.31	±4.63	±1.35	±19.40	±1.48	±0.079	±0.71

* For full key to traits see text

be significant, accounting for 98.6% of the total variation. The canonical vectors, corresponding to the seven significant latent roots and applying to the standardized data are given in table 7-8. Again the number of days to ear emergence was given heavy weighting in the derivation of the first axis as was 1000 corn weight. Very similar relative weightings were applied for the derivation of the second axis. For the third axis the trait height was given the heaviest weighting followed by grains per ear and yield.

Since the first two axes accounted for only 69.1% of the total variation, axes 1 and 2, 1 and 3 and 2 and 3 were plotted against each other (figures 7-4, 7-5 and 7-6). Figures 7-4 and 7-5 show that standard 14 (Akka) was far removed from the other standards with regard to the first canonical axis. No doubt this was due to the extreme earliness and high corn weight of this variety (table 7-7). Midas (5) was the latest standard and was the furthest removed from Akka in the two figures. The two points falling to the extreme left in both figures represent 6-rowed composite lines which had very low grain : straw ratios and were late and tall.

The standards Akka and Golden Promise occupied the two extreme positions on the third axis (figures 7-5 and 7-6). These represent the two extremes in height (table 7-7).

As in the first season the points representing the composite lines formed a scatter which overlapped that

TABLE 7-8

Canonical vectors applying to the standardized scores for traits measured in 1971

Traits	Canonical vectors						
	1	2	3	4	5	6	7
days to ear emergence	-1.7636	1.8467	-0.1393	0.2688	0.0058	0.0728	0.1727
height	-0.0579	0.1382	1.3493	-0.1033	-0.9816	-0.5385	-0.0824
head count	0.1215	0.1619	-0.3625	-0.0034	-0.1205	-0.6750	0.9299
mildew score	0.2032	-0.1838	0.0019	1.3493	-0.0027	-0.2087	-0.0985
yield	-0.1955	-0.0315	-0.6035	-0.4790	0.4600	-0.0093	-0.7256
grains per ear	-0.2864	-0.2598	0.8492	0.0763	1.2255	-0.2503	0.2543
grain: straw ratio	0.0361	0.2442	0.0930	0.2523	-0.1828	-0.7854	-0.3446
1000 corn weight	1.8822	1.6022	0.5532	0.3603	0.6277	0.0335	0.5159
% total variation	41.85	27.29	14.78	7.40	3.86	1.81	1.61

Figure 7-3 1970

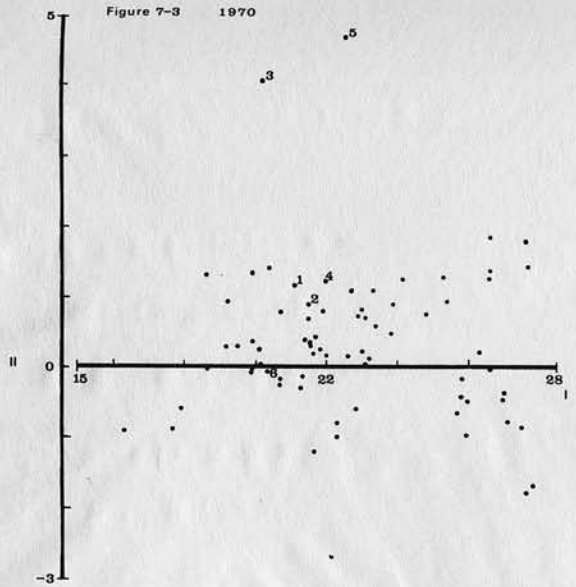


Figure 7-4 1971

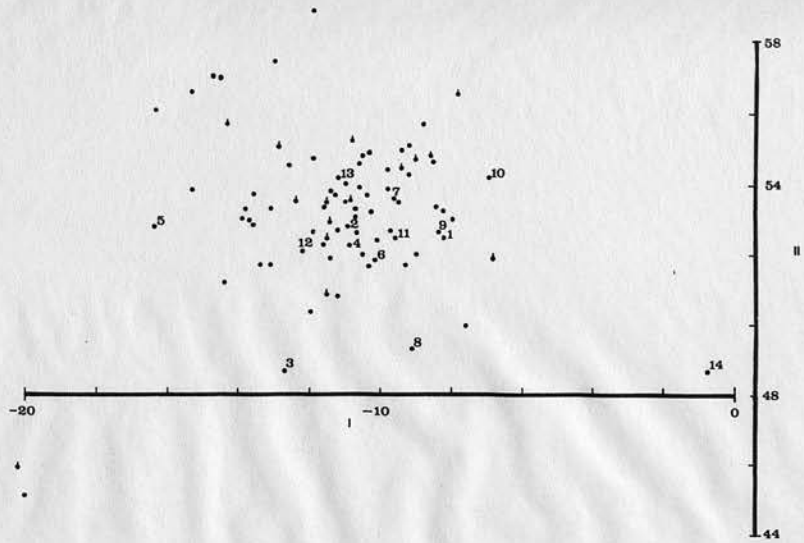


Figure 7-5 1971

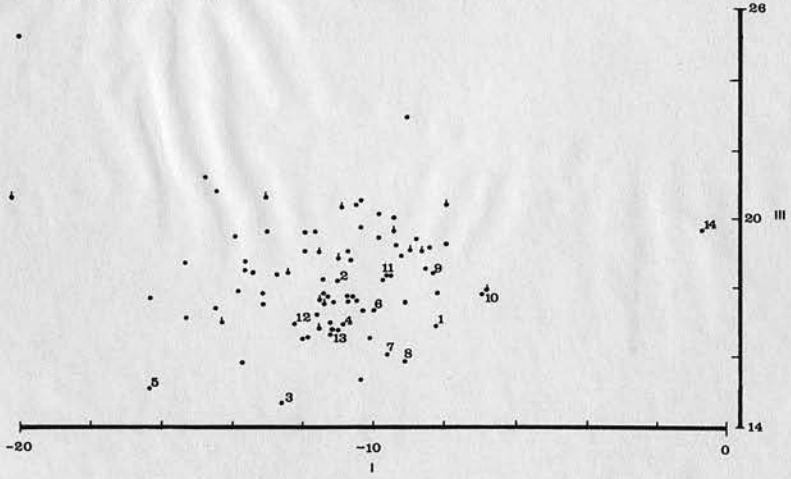
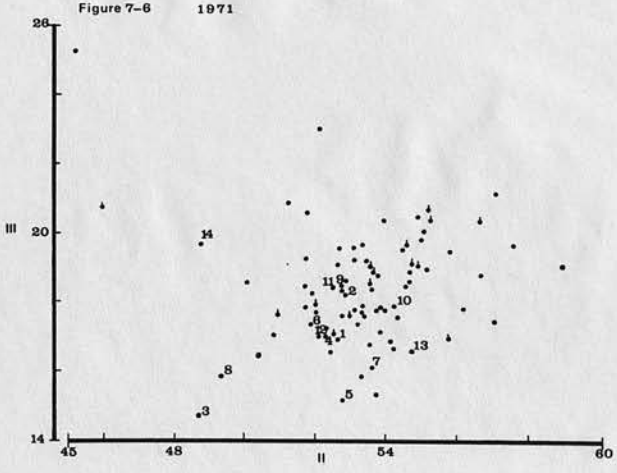


Figure 7-6 1971



For key to standards see table 7-7

♦ = Selections made in space defined by standards, 1970

TABLE 7-9

Values for seven canonical variates for fourteen standards from the analysis of seventy-two lines and fourteen standards grown in 1971

	Standard	Canonical variates 1	2	3	4	5	6	7
1.	Hassan	- 8.248	52.559	16.973	8.967	4.918	-11.696	9.424
2.	Ymer	-10.972	52.767	18.216	10.335	4.637	-12.355	8.969
3.	Golden Promise	-12.621	48.729	14.669	12.279	5.229	-11.659	8.412
4.	Sultan	-10.852	52.275	17.003	8.773	4.431	-12.431	9.169
5.	Midas	-16.357	52.806	15.189	8.517	4.925	-11.912	8.927
6.	Zephyr	-10.064	51.780	17.444	8.759	5.299	-12.335	8.403
7.	Julia	- 9.608	53.587	16.139	7.931	5.087	-11.768	8.761
8.	Berac	- 9.116	49.274	15.861	8.433	4.555	-12.311	8.547
9.	Cambrinus	- 8.280	52.681	18.485	9.245	4.960	-11.367	8.926
10.	Vada	- 6.955	54.188	17.871	8.211	5.640	-14.300	8.206
11.	Gerkra	- 9.564	52.474	18.415	7.690	4.699	-12.462	8.932
12.	Wing	-12.209	52.080	17.002	7.116	4.095	-12.249	8.696
13.	Deba Abed	-11.243	54.226	16.701	8.893	5.802	-12.904	8.743
14.	Akka	- 0.701	48.680	19.663	6.832	5.215	-11.780	9.985
	Latent roots	9.552	6.228	3.373	1.689	0.881	0.412	0.368

Extreme values of the range are underlined (disregarding Akka)

TABLE 7-10

Means for eight traits, measured in season 1971, for five lines selected in seasons 1970 and 1971

Line No.	Trait 1 Days	2 Height	3 Heads	4 Mildew	5 Yield*	6 Grains/ ear	7 Grain: straw	8 1000 Corn weight
160	55.0	94.0	50.8	4.15	215.9	24.32	0.77	39.87
272	57.0	99.3	53.4	7.85	212.6	23.15	0.76	42.40
424	57.8	98.4	56.2	6.20	237.7	26.15	0.97	42.50
698	56.0	94.9	56.4	2.30	218.6	23.90	0.95	42.72
760	59.0	97.8	49.0	5.90	204.9	23.72	0.80	40.25
S.E. selected lines	± 0.63	± 3.27	± 4.56	±1.330	± 19.14	± 1.459	±0.078	± 0.700
Means of selected lines	57.0	96.9	53.2	5.28	217.9	24.25	0.85	41.55
Means of Standards 1-13	55.7	91.5	50.7	4.45	212.7	23.29	0.87	41.81
Means of sixty-one unselected lines	57.5	101.31	48.45	5.83	204.9	25.19	0.77	42.36

* Mean yield (g) of two rows.

for the standards, though the fifteen lines selected on the basis of the six standards in 1970 showed no evidence of clustering.

As for the 1970 data, the range covered by the standards was determined (table 7-9). The variety Akka represented an extreme in the range for five of the seven canonical variates and when it was included twenty-four lines were selected, eight (33.3%) of which were lines which had been selected in the previous season as among the forty-five lines closest to the centroid of the acceptable space. When Akka was not considered eleven lines were selected, five (45.5%) of which were previous selections as within a group of twenty-six lines (2.9% of the total population) closest to the centroid of the acceptable space.

The means for the eight variates measured in 1971 for the five lines selected in both seasons are shown in table 7-10.

Season 1972

Forty-two selections at F_7 and seven control varieties were grown in a 7 x 7 lattice square design. The forty-two selections were as follows:

1 - 10	lines selected for yield from the sixty-nine lines grown in the replicated trial, 1970.
11 - 33	twenty-three lines selected by canonical analysis from the trial grown in 1971. These lines were selected when Akka was included amongst the standards.
34 - 42	lines from the trial of 1971 which were rejected by the canonical analysis but were taken forward because of their satisfactory yields.

The seven controls were Universe, Ymer, Midas, Golden Promise, Mazurka, Hassan, and CBRD(66)6, an unselected bulk at F_6 from the composite population which provided the selection material.

Adjusted mean yields are shown in Table 7-11. The poor yield of Mazurka was undoubtedly due to the bird damage which this variety sustained at ripening. None of the other treatments was significantly affected. As expected the unselected bulk CBRD(66)6 yielded poorly and the highest yielding line, CBRD(66)7/698 exceeded it by 23%. Perhaps largely because of the variability in yield between plots of Mazurka, the standard error for the difference between two adjusted treatment means is rather high. However, it cannot be but encouraging to note that lines have been selected with yields apparently close to those of Universe and Midas, varieties which have been amongst the top yielders in variety trials carried out in various parts of Scotland.

The second trial tested forty-three F_6 selections from the 900 lines grown in 1970. These lines were amongst the 233 selected in the acceptable space but were not grown in 1971. The controls were Julia, Golden Promise, Ymer, CBRD(66)6 and Mazurka. Except for Julia the controls were replicated four times within each of the three blocks.

Because the lines were not grown in 1971, seed quantities were limited and the plot size was therefore rather small. The main purpose was to assess the

TABLE 7-11

7 x 7 lattice square 1972

Adjusted mean yields in g m^{-2}

Treatment	Selection	Yield	Rank
1	CBRD(66)7/17	567	35 =
2	7/19	601	16 =
3	7/23	594	21
4	7/30	462	49
5	7/40	567	35 =
6	7/52	562	37
7	7/55	611	12
8	7/56	589	22 =
9	7/70	537	43
10	7/78	568	33
11	7/160	543	42
12	7/181	575	29
13	7/249	601	16 =
14	7/260	523	45
15	7/272	605	14 =
16	7/344	581	26
17	7/347	599	19 =
18	7/424	589	22 =
19	7/447	605	14 =
20	7/470	531	44
21	7/576	617	8 =
22	7/629	568	34
23	7/698	676	3
24	7/721	569	32
25	7/760	617	8 =
26	7/770	636	5
27	7/791	588	24
28	7/794	583	25
29	7/817	553	39
30	7/818	554	38
31	7/872	574	30
32	7/978	570	31
33	7/995	578	28
34	7/385	609	13
35	7/420	600	18
36	7/479	511	48
37	7/485	579	27
38	7/623	522	46
39	7/865	550	40
40	7/910	615	11
41	7/934	599	19 =
42	7/1013	617	8 =
43	Universe	689	1
44	Ymer	633	6
45	Midas	685	2
46	Golden Promise	627	7
47*	Mazurka	515	47
48	Hassan	650	4
49	CBRD(66)6	549	41

Average standard error of the difference between two adjusted treatment means is $\pm$ 37.86.

* This variety ripened early and suffered from bird damage.

TABLE 7-12

Randomized blocks 1972. Mean yields in g m^{-2} for controls and five best composite lines

Treatment	Yield	Rank
Julia	712	2
Golden Promise	590	36
"	546	54
"	614	27
"	517	60
Ymer	555	51
"	658	12
"	622	23
"	537	58
CBRD(66)6	706	3
"	677	7
"	641	18
"	662	10
Mazurka	575	42
"	609	30
"	560	47
"	671	8
CBRD(66)7/618	770	1
/624	703	4
/775	701	5
/478	692	6
/189	669	9

S.E. difference between two means ± 25.41

material visually but the randomized block design allowed an analysis of variance for yield to be carried out. The mean yields are given in table 7-12 for the controls and the five highest yielding lines. The line CBRD(66)6/618 significantly exceeded the yield of Julia, the best control and this line was 73rd in order of closeness to the centroid of the acceptable space in 1970 (8% of the population of 900 lines). The other lines listed in the table gave yields not significantly different from

that of Julia and all of these lines were amongst 17% of the 900 lines closest to the centroid of the acceptable space in 1970.

The replications within blocks for the controls showed very variable yields and the unselected bulk, CBRD(66)6, which ranked 41st out of 49 for yield in the lattice square, came 3rd, 7th, 18th and 10th for the mean yields over blocks for the four replications. It would be unwise therefore to attach too much significance to these figures but CBRD(66)6/618 and CBRD(66)6/189 (46th from the centroid of the acceptable space in 1970) were noted in the field for their promising appearance.

DISCUSSION

It has been claimed by Hazel and Lush (1942) and by Pesek and Baker (1969 a,b) that index selection is the most efficient method of improving several quantitative traits simultaneously. The object of index selection is to maximize the average "genetic worth" of a population and since genetic worth is the sum of products of the genotypic values of the measured traits and their respective economic weights, it reflects the overall value of a particular line or individual.

The problem which faces the plant breeder wishing to use a selection index is the difficulty of assigning economic weights to the traits, particularly when the "worth" of a trait and its absolute value are non-linearly related.

The selection method described here was developed in an attempt to circumvent these difficulties. Use of suitable standard varieties eliminates the need to apply selection criteria or to weight individual traits, whilst the alternative use of an acceptable range for each measured trait allows latitude in defining required gains.

Although it may be presumed that all the traits measured by the plant breeder will have some economic significance, the analysis will apply its own relative weightings to maximize the discrimination between lines. These weightings may not be those the breeder might have applied intuitively but they will produce the best possible discrimination. The inclusion of carefully chosen standard varieties in the analysis allows an assessment of the relative positions of the lines under selection.

A criticism of this procedure might be that it could result in the rejection of lines which are superior to the standard varieties. However, it has already been noted that the transformation to canonical variates of the acceptable range for each trait may result in a multi-dimensional region which is somewhat larger than that defined by the limits applied to the untransformed data. Thus a line which falls outside the range for a particular trait may nevertheless be included in the transformed acceptable range if it is satisfactory with regard to a trait or traits to which the analysis applies heavy weighting.

In the results described here the standard varieties performed poorly in 1970 relative to the population under selection and an "ideal" space was defined using an acceptable range for each trait. However, this space appeared to be too big and selection pressure was increased by favouring those lines which fell nearest the centroid of the acceptable space. In the 1971 experiment, more standards were included and thirteen of these were used to define the range for each canonical variate within which lines were selected. The five lines selected in both 1970 and 1971 were found to have been among a small group of lines (2.9% of the population) nearest the centroid of the acceptable space in 1970.

Because the effect of the analysis is to discriminate groups regardless of their worth to the plant breeder, it is essential that care should be taken in the choice of traits to be measured. Trivial separation of groups may result if a measurement implicitly demonstrates a known and obvious separation. Unless the breeder specifically requires such a classification measurements of this type should be omitted.

The consistency of performance of lines, selected by the method, over seasons will be obscured by genotype x season interaction, so that lines selected in one season may not necessarily perform well relative to the standards in the next, though this may well depend upon the heritability of the trait under consideration. In this work

the main object was to select high yielding lines from the composite material but these were required, nevertheless, to conform to certain agronomic criteria. Yield, of course, cannot be accurately assessed in trials with small plots and few replications but if the other traits are carefully chosen it might be expected that selected lines would produce high yields.

In these experiments the potential, not only of the method of selection, but also of the composite material was being explored. The results from the yield trials in 1972, particularly those from the lattice square experiment, showed that this composite population is indeed a promising source of high yielding material even at such an early stage in its development. The initial selection of single plants from an F_4 population was no doubt premature and greater success might have been achieved had the population been more advanced.

CHAPTER 8

CONCLUSIONS

The work described in this thesis has been entirely concerned with the analysis of quantitative data. Such an objective approach should perhaps lead to objective conclusions and we must try to answer the inevitable question - how do these results help the barley breeder?

The answer to this question must obviously be restricted by limitations in the experiments and in the amount of material sampled. Thus it was pointed out in Chapter 2 that the parents chosen for the diallel experiments described in this thesis should be regarded as a fixed set, and that inferences drawn from the experiments refer strictly only to the population under study. Again, the traits measured exhibited continuous variation and were handled by biometrical methods which do not tell us anything about the properties of individual genes but, rather, about the effects of gene aggregates. As far as the diallel experiments are concerned then, the questions we might reasonably ask are - what have we learned about the inheritance of the traits studied which can perhaps be generalized? and - what facts have the analyses revealed, about the parents under study, which can be exploited by the barley breeder?

Estimates of the heritability of the main components of yield have been obtained and whilst it has been noted

(Chapter 5) that the absolute values for such estimates must be considered as specific to the experimental conditions for which they were made, nevertheless the relative heritabilities for each trait are of more general interest.

The extensive data obtained from these experiments, together with the separation of environmental from genetic variance, have allowed the calculation of genotypic, phenotypic and environmental covariances between traits (tables 5-3, 5-4, 5-5 and 5-6). Again, it has to be allowed that the relationships which were found between traits in this population may not necessarily be found in a different population, particularly if this population had not been strongly selected. However, some of the findings confirmed those of other authors and it was perhaps particularly significant that no strong negative correlations were found between the three yield components in the 2-rowed material since this might be expected if the physiological limits to yield had been reached. It is reasonable to suppose that the possibilities for further improvement of individual yield components detected in this material would exist also in other material of similar performance.

Diallel analyses have shown that the components of yield were not determined entirely by genes behaving additively but that the action of dominant genes could be detected. This does not mean that high expression of these traits could not easily be fixed, but in the choice

of parents account must be taken of the non-additive action of some genes. The progeny of a cross between a parent carrying mostly dominant genes for a trait and a parent carrying mostly recessive genes, as indicated by the Wr, Vr analysis would be expected to segregate widely in F_2 and to demonstrate considerable genetic variance.

Of the information derived from the diallel analysis about the parents, the most salient points are summarized below.

Olli	The earliest genotype for days to heading and carries mostly dominant genes for early heading; mostly recessive genes for number of grains per ear; mostly recessive genes for corn weight.
Pirkka	Fewer dominant genes for days to heading than Olli; mostly recessive genes for number of grains per ear; mostly recessive genes for corn weight.
Cambrinus	Mostly dominant genes for corn weight; mostly dominant genes for number of grains per ear but negative general combining ability for this trait.
Ymer	Mostly recessive genes for days to heading; carries dominant genes for number of grains per ear but low expression for this trait; mostly dominant genes for corn weight.
Deba Abed	Possibly carries dominant genes for days

to heading; mostly recessive genes for number of grains per ear but very high expression of this trait; fairly high positive general combining ability for number of grains per ear and high specific combining ability with Boreham Warrior for this trait; mostly dominant genes for corn weight.

Scotch Bere — Mostly recessive genes for heading date; fewer recessive genes for number of grains per ear than the other 6-rowed genotypes; apparently dominant genes for corn weight.

O.A.C. 21 — Mostly recessive genes for heading date; mostly recessive genes for number of grains per ear; mostly recessive genes for corn weight.

Golden Promise — Mostly dominant genes for number of grains per ear but intermediate expression; strong negative specific combining ability with Midas for this trait; mostly recessive genes for corn weight and very low expression.

Maris Baldric — Mostly recessive genes for number of days to heading; possibly carries dominant genes for tiller number; mostly dominant genes for corn weight and fairly high positive general combining ability for this trait.

Midas — Showed interaction with several of the other genotypes for days to heading; a late genotype showing strong positive general combining ability for this trait; mostly dominant genes for number of grains per ear and exhibits a high expression of this trait together with a strong positive general combining ability; strong negative specific combining ability with Golden Promise for number of grains per ear; mostly recessive genes for corn weight and strong negative general combining ability; strong positive specific combining ability with Mosane for corn weight.

Mosane — Apparently equal proportions of dominant and recessive genes for days to heading, tiller number and number of grains per ear; negative general combining ability for number of grains per ear but strong positive specific combining ability with Boreham Warrior; mostly dominant genes for corn weight with strong negative general combining ability; good specific combining ability with Midas for this trait.

Sultan — Apparently mostly recessive genes for days to heading; fairly strong positive general combining ability for tiller

number; strong negative general combining ability for number of grains per ear; mostly dominant genes for corn weight.

Boreham Warrior — Mostly recessive genes for days to heading and strong positive general combining ability. Apparently equal proportions of dominant and recessive genes for number of grains per ear and high expression; strong positive general combining ability in one season for grains per ear and strong specific combining ability with Mosane; mostly dominant genes for corn weight and strong positive general combining ability.

In drawing general conclusions about the parents, attention must be drawn to the differences between the three North American 6-rowed varieties on the one hand and the local 6-rowed variety, Scotch Bere on the other hand. Whereas the former varieties were shown to carry mostly recessive genes for the traits grains per ear and corn weight, Scotch Bere apparently carried a higher proportion of dominant genes for grains per ear and, although falling well off the regression line in figure 4-12, apparently carried mostly dominant genes for corn weight. In general, apart from the obvious 6-rowed character of the ear, Scotch Bere more nearly resembled the 2-rowed genotypes, in the main components of yield, than the other 6-rowed genotypes.

It is interesting to note (tables 4-1, 4-11 and 4-23) that parents which exhibited high expression of a particular yield component sometimes also exhibited low expression of another component. Thus Midas produced a large number of grains per ear but had a low corn weight. Again, Sultan gave a high tiller count but had very low numbers of grains per ear. Whilst this phenomenon was not common to all the varieties, it does suggest that within a genotype compensatory mechanisms may exist between the levels of expression of the individual components of yield even though, as remarked earlier, negative correlations between yield components could not be shown when data for all parents and hybrids were pooled.

Turning to the choice of parents, and considering only 2-rowed parents, tables 4-10a, 4-10b, 4-18, 4-19, 4-20, 4-32 and 4-33 show combining ability estimates and have provided considerable information in deciding which crosses should be taken further in the breeding programme.

Tiller number, as has been remarked previously, had a low narrow-sense heritability in this material and need not be considered very important in the choice of parents, though Sultan and Mosane might be chosen as having reasonably high general combining abilities.

Boreham Warrior and particularly Midas exhibited strong general combining ability for number of grains per ear, and the particular hybrid combination of Boreham Warrior with Mosane showed good specific combining ability in both seasons. The crosses Midas x Golden Promise and

Deba Abed x Mosane however, showed strong negative specific combining ability.

The crosses Midas x Golden Promise and Deba Abed x Mosane again exhibited strong negative specific combining ability for the trait 1000 corn weight in 1971. However, Midas x Mosane, Midas x Deba Abed and Golden Promise x Maris Baldric would seem to be promising if high 1000 corn weight were required in the progeny. Both Maris Baldric and Boreham Warrior showed good general combining ability for this trait in 1971.

Reference to tables 5-10, 5-11 and 5-12 confirms that the parental combinations mentioned above as having high specific combining ability for a particular trait generally produced F_2 progeny with high means and high genetic variability for further selection.

It was found that in general dominance acted in a positive direction i.e. towards higher expression of the main components of yield. Continued selection within such a population should eventually result in the fixation of dominant genes. The varieties under study appear to represent various stages in this process. Deba Abed is remarkable, however, in having a large number of grains per ear but apparently carrying mostly recessive genes for this trait (figures 4-10 and 4-11).

The canonical analyses applied to the diallel data confirmed some of the findings from the biometrical analyses and also grouped the parents according to their similarities and differences. The scatter diagrams

suggested that with each generation of selfing the positions of the hybrids would more nearly approach the mid-parental positions, so that the position of an F_4 progeny from a single cross, for instance, could be reasonably well predicted. It follows that the progeny of parents grouped closely together may be virtually indistinguishable from the parents and that more significant gains might accrue by crossing parents placed rather far apart by the analysis. No confirmation of this hypothesis was possible in the work described here but it does suggest a possible approach in a hybridization programme.

The selection method described in Chapter 7 was not only a research investigation but a practical attempt to select promising lines from a composite cross population. Conclusions were drawn at the end of that chapter and little else need be said here.

On the whole it may be concluded that canonical analysis can be a useful tool to the plant breeder whether he wishes to use it for selection purposes or merely as a means of classifying or distinguishing between the materials at his disposal.

The selection method described represents merely a dip into a population containing a very wide range of genetic variability. Several selections were made which might eventually become new varieties in their own right or will at least be used as parents in the breeding programme. It is to such populations, with their wealth

of variability, that barley breeders should perhaps look if they are to obtain the large advances for which they are searching.

LITERATURE CITED

ÅBERG, E. 1940. The taxonomy and phylogeny of Hordeum L. Sect. Cerealia Ands. Symb. bot. upsal. 4, No. 2, 1-156.

ÅBERG, E. and WIEBE, G. A. 1945. Irregular barley, Hordeum irregulare, sp. nov. J. Wash. Acad. Sci. 35, 161-164.

AKSEL, R. and JOHNSON, L. P. V. 1961. Genetic studies on sowing-to-heading and heading-to-ripening periods in barley and their relation to yield and yield components. Can. J. Genet. Cytol. 3, 242-259.

ALLARD, R. W. 1961. Relationship between genetic diversity and consistency of performance in different environments. Crop Sci. 1, 127-133.

ALLARD, R. W. and JAIN, S. K. 1962. Population studies in predominantly self-pollinated species. II Analysis of quantitative changes in a bulk hybrid population of barley. Evolution 16, 90-101.

ALLARD, R. W., JAIN, S. K. and WORKMAN, P. L. 1968. The genetics of inbreeding populations. Adv. genet. 14, 55-131.

ANON. 1971. Guide for the assessment of cereal diseases. Plant Pathology Laboratory, Harpendon, Herts., England.

BEAVEN, E. A. 1947. Barley. Fifty years of observation and experiment. London: Duckworth.

BELL, G. D. H. 1951. Barley breeding and related researches. J. Inst. Brew. 57, 247-260.

BELL, G. D. H. 1964. Breeding techniques - general techniques. Proc. 1st Int. Barley Genetics Symp. Wageningen. 1963, 285-302.

BELL, G. D. H. 1965. The comparative phylogeny of the temperate cereals. In Essays on Crop Plant Evolution. Ed. Sir Joseph Hutchinson. Cambridge University Press. 70-102.

BELL, G. D. H. and LUPTON, F. G. H. 1962. The breeding of barley varieties. In Barley and Malt. 45-99. Ed. A. H. Cook. New York: Academic Press.

BENNETT, E. 1965. Plant introduction and genetic conservation: genecological aspects of an urgent world problem. Scottish Pl. Breed. St. Rec. 27-113.

BINGHAM, J. 1971. Physiological objectives in breeding for grain yield in wheat. In The Way Ahead in Plant Breeding. Proc. 6th Cong. of Eucarpia, Cambridge. 15-29.

BLACKITH, R. E. and REYMENT, R. A. 1971. Multivariate Morphometrics. London and New York: Academic Press.

BREESE, E. L. 1956. The genetical consequences of assortative mating. Heredity 10, 323-343.

BRITTON, D. K. 1969. Cereals in the United Kingdom, Production, Marketing and Utilization. London: Pergamon Press.

CATON-THOMPSON, C. and GARDNER, E. W. 1926. The recent geology and neolithic industry of the Northern Fayum Desert. Jl R. anthrop. Inst. 301-323.

CRUMPACKER, D. W. and ALLARD, R. W. 1962. A diallel cross analysis of heading date in wheat. Hilgardia 32, 275-318.

DROS, J. 1957. The creation and maintenance of two spring barley varieties. Euphytica 6, 45-48.

DUDLEY, J. W. and MOLL, R. H. 1969. Interpretation and use of estimates of heritability and genetic variances in plant breeding. Crop Sci. 9, 257-262.

EAVES, L. J. and BRUMPTON, R. J. 1972. Factors of co-variation in Nicotiana rustica. Heredity 29, 151-175.

EISENHART, C. 1947. The assumptions underlying the analysis of variance. Biometrics 3, 1-21.

FIUZAT, Y. and ATKINS, R. E. 1953. Genetic and environmental variability in segregating barley populations. Agron. J. 45, 414-420.

FRANKEL, O. H. 1950. The development and maintenance of superior genetic stocks. Heredity 4, 89-102.

FYFE, J. L. and GILBERT, N. 1963. Partial diallel crosses. Biometrics 19, 278-286.

GILBERT, N. 1958. Diallel cross in plant breeding. Heredity 12, 477-492.

GRAFIUS, J. E. 1959. Heterosis in barley. Agron. J. 51, 551-554.

GRAFIUS, J. E. 1963. Vector analysis applied to crop eugenics and genotype-environment interaction. In Statistical Genetics and Plant Breeding. NAS-NRC 982, 197-217.

GRAFIUS, J. E. 1964. Breeding for yield. In Barley Genetics I, Proc. 1st Int. Barley Genetics Symp. Wageningen, 267-276.

GRAFIUS, J. E. 1965. A geometry of plant breeding. Mich. St. Univ. Res. Bull. 7.

GRAFIUS, J. E. and WIEBE, G. A. 1959. Expected genetic gain in yield in small grain. A geometrical interpretation. Agron. J. 51, 560-562.

GRIFFING, B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. Aust. J. biol. Sci. 9, 463-493.

HANSON, W. D. 1963. Heritability. In Statistical Genetics and Plant Breeding. NAS-NRC 982, 125-140.

HARLAN, H. V. and MARTINI, M. L. 1929. A composite hybrid mixture. J. Am. Soc. Agron. 21, 487-490.

HARLAN, H. V. and MARTINI, M. L. 1938. The effect of natural selection in a mixture of barley varieties. J. Agric. Res. 57, 189-199.

HARLAN, J. R. 1956. Distribution and utilization of natural variability in cultivated plants. Brookhaven Symp. Biol. 9, 191-208.

HASHIGUCHI, S. and MORISHIMA, H. 1969. Estimation of genetic contribution of principal components to individual variates concerned. Biometrics 25, 9-15.

HAYES, J. D. 1965. A study of early generation assessment in cereals with particular reference to barley. PhD thesis, University of Wales.

HAYES, J. D. 1968. The genetic basis of hybrid barley production and its application in Western Europe. In Cereal Improvement, Euphytica Suppl. 1, 87-102.

HAYMAN, B. I. 1954a. The theory and analysis of diallel crosses. Genetics 39, 789-809.

HAYMAN, B. I. 1954b. The analysis of variance of diallel tables. Biometrics 10, 235-244.

HAYMAN, B. I. 1957. Interaction, heterosis and diallel crosses. Genetics 42, 336-355.

HAYMAN, B. I. 1958. The theory and analysis of diallel crosses II. Genetics 43, 63-85.

HAZEL, L. N. and LUSH, J. L. 1942. The efficiency of three methods of selection. J. Hered. 11, 393-402.

HENDERSON, C. R. 1963. Selection index and expected genetic advance. In Statistical Genetics and Plant Breeding. NAS-NRC 982, 141-163.

HOLLAND, D. A. 1968. Component analysis: an aid to the interpretation of data. Expl. Agric. 5, 151-164.

HOPE, K. 1968. Methods of Multivariate Analysis. Unibooks, University of London Press Ltd.

HORNE, F. R. 1961. Prospects for crop improvement through new varieties and better seeds. J. Fmrs' Club Pt I.

HUNTER, H. and LEAKE, H. M. 1933. Recent Advances in Agricultural Plant Breeding. London: J. & A. Churchill.

IMMER, F. R. 1942. Distribution of yields of single plants of varieties and F_2 crosses of barley. J. Am. Soc. Agron. 34, 844-850.

JACKSON, A. 1933. Egyptian neolithic barley. Nature 131, 652.

JAIN, S. K. and ALLARD, R. W. 1960. Population studies in predominantly self-pollinated species. I. Evidence for heterozygote advantage in a closed population of barley. Proc. natn. Acad. Sci. U.S.A. 46, 1371-1377.

JANA, S. and SEYFFERT, W. 1972. Simulation of quantitative characters by genes with biochemically definable action. IV The analysis of heritable variation by the diallel technique. T.A.G. 42, 16-24.

JINKS, J. L. 1954. The analysis of continuous variation in a diallel of Nicotiana rustica varieties. Genetics 39, 767-788.

JINKS, J. L. 1955. A survey of the genetical basis of heterosis in a variety of diallel crosses. Heredity 9, 223-238.

JINKS, J. L. 1956. The F_2 and backcross generations from a set of diallel crosses. Heredity 10, 1-30.

JINKS, J. L. and HAYMAN, B. I. 1953. The analysis of diallel crosses. Maize Genet. Coop. News Lett. 27, 48-54.

JINKS, J. L. and JONES, R. M. 1958. Estimation of the components of heterosis. Genetics 43, 223-234.

JOHNSON, L. P. V. and AKSEL, R. 1959. Inheritance of yielding capacity in a fifteen-parent diallel cross of barley. Can. J. Genet. Cytol. 1, 208-265.

JONES, D. F. 1917. Dominance of linked factors as a means of accounting for heterosis. Genetics 2, 466-479.

JONES, R. M. 1965. Analysis of variance of the half diallel table. Heredity 20, 117-121.

KEARSEY, M. J. 1965. Biometrical analysis of a random mating population: a comparison of five experimental designs. Heredity 20, 205-235.

KEMPTHORNE, O. 1956. The theory of the diallel cross. Genetics 41, 451-459.

KRZANOWSKI, W. J. 1972. Techniques in multivariate analysis. In The Way Ahead in Plant Breeding, Proc. 6th Cong. of Eucarpia, Cambridge 147-155.

LAMBERT, J. W. and LIANG, T. J. 1952. Studies of various characters of six-rowed segregates from crosses between two-rowed and six-rowed barleys. Agron. J. 44, 364-369.

LEE, B. T. O. and PARSONS, P. A. 1968. Selection, prediction and response. Biol. Rev. 43, 139-174.

LUPTON, F. G. H. 1961. Studies in the breeding of self-pollinating cereals. 3. Further studies in cross prediction. Euphytica 10, 209-224.

LUPTON, F.G.H. 1969. Estimation of yield in wheat from measurements of photosynthesis and translocation in the field. Ann. appl. Biol. 64, 363-374.

LUPTON, F. G. H. 1972. Further experiments on photo-synthesis and translocation in wheat. Ann. appl. Biol. 71, 69-79.

LUPTON, F. G. H. and WHITEHOUSE, R. N. H. 1957. Studies on the breeding of self-pollinating cereals. 1. Selection methods in breeding for yield. Euphytica 6, 169-184.

LUPTON, F. G. H., ALI, MOHAMED A. M. and SUBRAMANIAM, S. 1967. Varietal differences in growth parameters of wheat and their importance in determining yield. J. agric. Sci., Camb. 69, 111-123.

MATHER, K. 1949. Biometrical Genetics. London: Methuen & Co. Ltd.

MATHER, K. and VINES, A. 1952. The inheritance of height and flowering time in a cross of Nicotiana rustica. In Quantitative Inheritance 49-80. London: H.M.S.O.

MATHER, K. and JINKS, J. L. 1971. Biometrical Genetics. London: Chapman and Hall Ltd.

NAMKOONG, G. 1966. Statistical analysis of introgression. Biometrics 22, 488-502.

PERKINS, JEAN M. 1972. The principle component analysis of genotype-environmental interactions and physical measures of the environment. Heredity 29, 51-70.

PESEK, J. and BAKER, R. J. 1969 a. Comparison of tandem and index selection in the modified pedigree method of breeding self-pollinated species. Can. J. Pl. Sci. 49, 773-781.

PESEK, J. and BAKER, R. J. 1969 b. Desired improvement in relation to selection indices. Can. J. Pl. Sci. 49, 803-804.

RAO, C. R. 1952. Advanced Statistical Methods in Biometric Research. New York: Wiley.

RASMUSSON, D. C. 1966. Potential for hybrid barley in relation to seed costs. Barley Newsletter 9, 18-20.

REYMENT, R. A. 1969. A multivariate palaeontological growth problem. Biometrics 25, 1-8.

RIGGS, T. J. and HAYTER, A. M. 1972. Diallel analysis of the time to heading in spring barley. Heredity 29, 341-357.

ROBINSON, H. F., COMSTOCK, R. E. and HARVEY, P. H. 1951. Genotypic and phenotypic correlations in corn and their implications in selection. Agron. J. 43, 283-287.

SCHMIDT, J. 1919. La valeur de l'individu à titre de générateur appéciée suivant la méthode du croisement diallèle. C. r. Lab. Carlsberg 14, No. 6, 33 -

SEAL, H. L. 1964. Multivariate Statistical Analysis for Biologists. London: Methuen & Co. Ltd.

SHUKLA, G. K. 1972. Application of some multivariate techniques in the analysis and interpretation of the genotype-environment interaction. Unpublished paper read at symposium on genotype-environment interactions, Birmingham University. September, 1972.

SIMMONDS, N. W. 1962. Variability in crop plants, its use and conservation. Biol. Rev. 37, 422-465.

SIMMONDS, N. W. 1968. The cereal breeding situation. Rep. Scottish Pl. Breed. Stn. 1967-68, 16-34.

SMITH, H. F. 1936. A discriminant function for plant selection. Ann. Eugen. 7, 240-250.

SUNESON, C. A. 1949. Survival of four barley varieties in a mixture. Agron. J. 41, 459-461.

SUNESON, C. A. 1951. Male sterile facilitated synthetic hybrid barley. Agron. J. 43, 234-236.

SUNESON, C. A. 1956. An evolutionary plant breeding method. Agron J. 48, 188-191.

SUNESON, C. A. 1960. Genetic deversity - a protection against plant diseases and insects. Agron. J. 52, 319-321.

SUNESON, C. A. and WIEBE, G. A. 1942. Survival of barley and wheat varieties in mixtures. Agron J. 34, 1052-1056.

TAKAHASKI, R. 1955. The origin and evolution of cultivated barley. Adv. Genet. 7, 227-266.

THOMAS, R. L., GRAFIUS, J. E. and HAHN, S. K. 1971 a. Genetic analysis of correlated sequential characters. Heredity 26, 177-188.

THOMAS, R. L., GRAFIUS, J. E. and HAHN, S. K. 1971 b. Transformation of sequential quantitative characters. Heredity 26, 189-193.

WALKER, J. T. 1969. Selection and quantitative characters in field crops. Biol. Rev. 44, 207-243.

WEINHUES, F. 1968. Long-term yield analysis of heterosis in wheat and barley: variability of heterosis, fixation of heterosis. In Cereal Improvement, Euphytica suppl. 1, 49-62.

WHITEHOUSE, R. N. H. 1968. Barley breeding at Cambridge. Rep. Pl. Breed. Inst., Cambridge. 1968, 6-29.

WHITEHOUSE, R. N. H. 1970 a. An application of canonical analysis to plant breeding. Proc. 5th Congr. Eucarpia, Milano 61-96.

WHITEHOUSE, R. N. H. 1970 b. Canonical analysis as an aid in plant breeding. In Barley Genetics II, Proc. 2nd Int. Barley Genetics Symp. Washington 269-282

WHITEHOUSE, R. N. H., THOMPSON, B. and RIBEIRO, M. A. M. de V. 1958. Studies on the breeding of self-pollinating cereals, 2. The use of the diallel cross analysis in yield prediction. Euphytica 7, 147-169.

WILLIAMS, W. 1959. Heterosis and the genetics of complex characters. Nature 184, 527-530.

YATES, F. 1947. Analysis of data from all possible reciprocal crosses between a set of parental lines. Heredity 1, 287-307.

YOUNG, S. S. Y. 1961. A further example of the relative efficiency of three methods of selection for genetic gains under less restricted conditions. Genet. Res. 2, 106-121.

ZOHARY, D. 1960. Studies on the origin of cultivated barley. Bull. Res. Coun. Israel 9D, 21 -
v

ZUKOVSKIJ, P. M. 1950. Cultivated Plants and their Wild Relatives. Abridged translation by P. S. Hudson, C. A. B. publication.

APPENDIX I

THE PHYLOGENY AND EVOLUTIONARY DEVELOPMENT OF THE CULTIVATED BARLEYS

The genus Hordeum has a basic chromosome number of seven and comprises about twenty-five species which have been classified (Åberg, 1940) into the following four sections: Stenostachys Nevski, Campestria Ands., Bulbohordeum Nevski and Cerealia Ands. The first three sections are comprised of various perennial or annual wild species, some of which are polyploid and all of which have small grains. It is therefore unlikely that any cultivated form could have arisen from the wild species belonging to these sections (Takahashi, 1955).

The section Cerealia contains the cultivated forms and two kinds of wild barley. Åberg and Wiebe (1945) classified them on the basis of brittleness of rachis and number of kernel rows per ear as follows:

Hordeum agriocrithon E. Åberg	ear brittle, six-row
H. spontaneum C. Koch	ear brittle, two-row
H. vulgare L.emend.Lam.	ear tough, six-row
H. distichum L.emend.Lam.	ear tough, two-row
H. irregulare Åberg et Wiebe	ear tough, kernel row irregular.

The wild two-rowed species, H. spontaneum was first described by Koch in 1848 and is similar in many respects to some of the cultivated forms of H. distichum except that it is characterised by fragility of the rachis,

long rough awns, densely haired empty glumes and an extremely long period of dormancy of the seeds. H. spontaneum was the only wild species known until the discovery in 1938 of the six-rowed H. agriocrithon. Kernels of this barley were first found in a sample of wheat from East Tibet and subsequently several more seeds were found among samples of other cereals from central and southern Tibet. The close morphological similarity of the two wild species of barley to the cultivated types indicates that they should have similar genetic constitutions. However, the question as to which is more primitive, agriocrithon or spontaneum, has been the subject of much controversy.

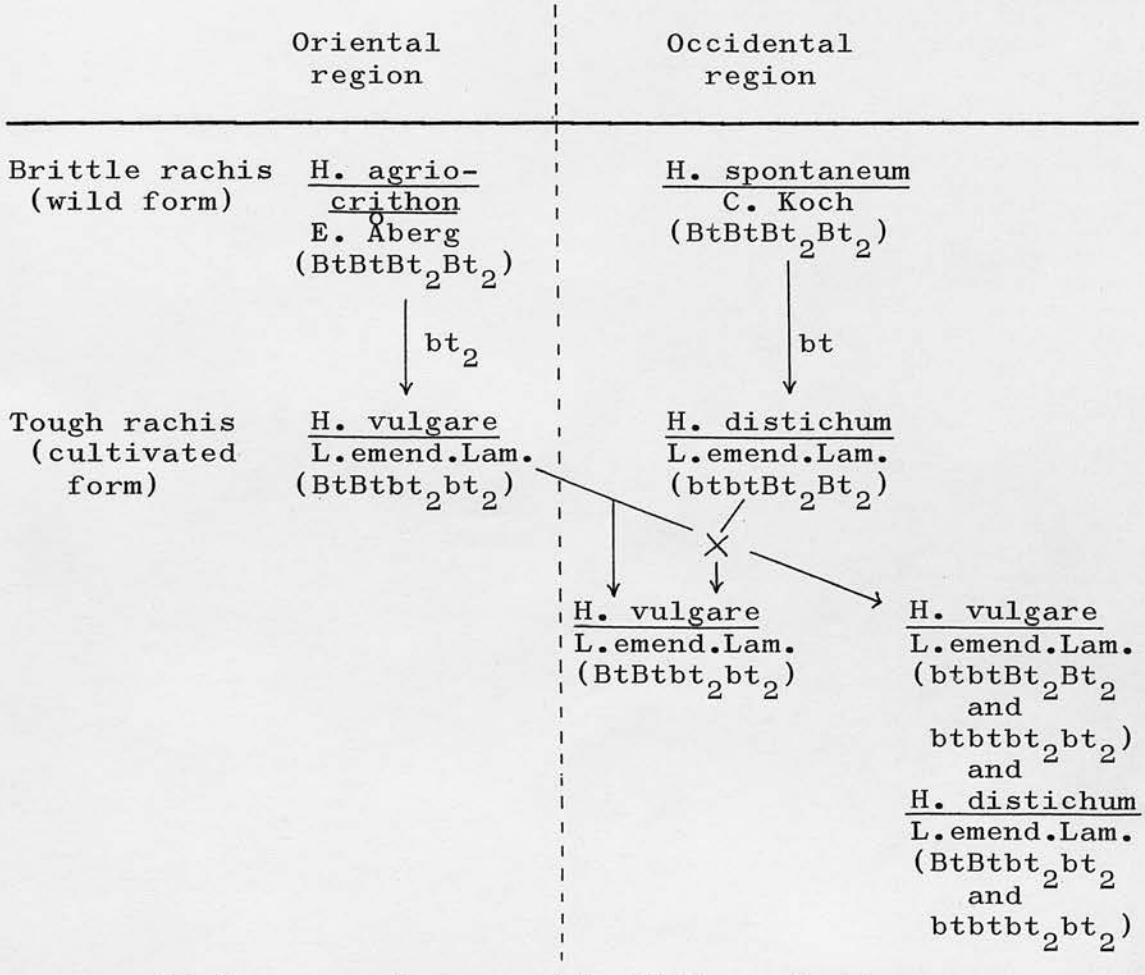
Žukovskij (1950) and Takahashi (1955) state that the six-rowed barleys are older than the two-rowed barleys and that the grains found in the neolithic and bronze age deposits and those of ancient Egypt were exclusively of six-rowed origin. The oldest authentic records of a two-rowed barley are believed to be among the Greek and Roman archives of about 300 B.C. (Bell, 1965). Again, the six-rowed character does appear logically the primitive condition since rudimentation is more probable than the reverse. Jackson (1933) claimed that stores of grain, found in Egypt during excavations by Caton-Thompson and Gardner (1926), which must have been grown between 5000 and 6000 B.C., contained two-rowed and six-rowed barley varieties. This was probably incorrect however (Beaven, 1947) and it seems more likely that the barley sample

was entirely of a six-rowed type. Zohary (1960) maintained that *agriocrithon* is a derived form and that the six-rowed forms arose only subsequent to the origin of two-rowed cultivated forms with a tough rachis. Certainly *agriocrithon* has a limited distribution but this need not mean that the ancient primitive wild barley was not a six-rowed type (Bell, 1965).

A monophyletic origin for the cultivated barleys is not the only possibility. Mutation from the wild-type brittle rachis to the tough rachis characteristic of cultivated forms must have been the main evolutionary step and brittle rachis is determined by two complementary genes, *Bt* and Bt_2 with the tough rachis condition being determined by either or both of the recessive alleles (Johnson and Åberg, 1943). *H. agriocrithon* and *H. spontaneum* have the same genetic constitution, $BtBtBt_2Bt_2$, while among the cultivated barleys there are three kinds of genotype, $BtBtbt_2bt_2$ (or type 'E'), $btbtBt_2Bt_2$ (type 'W') and $btbtbt_2bt_2$ (type 'we'). Takahashi (1955) showed from the results of a survey of cultivated barleys in various regions of the world, that most of the varieties tested were either of type E or type W with only a very few of type we. Further, the barleys of the Oriental region were almost entirely of type E whilst those of the Occidental region were 60%-80% type W, 20%-40% type E and a very few type we. The distribution of *bt* and bt_2 genes in the Oriental and Occidental regions was similar to that of the two-rowed and six-rowed characters,

indicating the existence of two lines of descent in the cultivated barleys.

Such results led Takahashi to postulate a diphyletic origin as shown:



Phylogeny and geographic differentiation in cultivated barleys.

from Takahashi (1955).

According to this, primitive cultivated forms differentiated by mutation of Bt_2 to bt_2 in H. agriocrithon somewhere in East Asia. These cultivated forms and their

derivatives spread over various parts of the world. Subsequently, two-rowed cultivated forms appeared by mutation of Bt to bt in H. spontaneum growing in south-western Asia. These two-rowed cultivated forms crossed with varieties of six-rowed type E and resulted in various new two-rowed and six-rowed forms.

It is interesting to note (Bell, 1965) the survival and spread under cultivation and utilization, of the pigmentless, hulled, awned forms whilst the forms with special modifications such as naked grain, hooded florets and various expressions of colour in grains and hulls, have persisted only in restricted areas and often associated with primitive agriculture.

Such is the richness of genetic variability within the section Cerealia of the genus Hordeum that the development of improved genotypes by plant breeders has been, and will no doubt continue to be highly successful.

APPENDIX II

COMPOSITE CROSS POPULATIONS

Composite cross populations in the inbreeding cereals have been mainly developed and evaluated in America, the work on barley being pioneered by Harlan and Martini in California (Harlan and Martini, 1929). These workers crossed twenty-eight varieties of barley in all combinations and made up a population composed of equal amounts of F_2 seed from each cross.

Suneson (1956) described a study involving four composite cross populations one of which, CC II, was the population set up by Harlan and Martini and had reached the F_{29} generation. Another of the populations, CC XIV, contained a gene for male-sterility (Suneson, 1951) which allowed continuing gene recombinations through natural crossing. Each of the populations contained the standard Californian barley variety, Atlas. The populations were grown each year with no intentional selection, and progressive yield improvement, relative to the control variety Atlas, was noted with successive generations. The CC XIV population, which yielded 88% of Atlas at F_2, reached the same yield as this variety by the F_9 generation, whereas CC II, which yielded 68% of Atlas at F_3, did not equal the control until the F_{20} generation. Atlas itself appears to have been more susceptible to environmental fluctuations than the composite

populations and its yield was very variable. However, the evidence supported the contention that natural selection could produce populations as productive as breeders' improved varieties though the control variety in this case had no doubt been superseded by higher yielding varieties by the time the composite populations began to equal it in yield. It also emerged from this work that lines superior to Atlas could be selected from the populations and that the number of promising lines selected was greater in the more advanced generations. Thus the populations, requiring very little effort for their maintenance, proved to be valuable sources of breeding material.

Allard and Jain (1962) studied CC V, developed by Harlan from intercrosses of thirty-one varieties, and measured the means and variances for heading time and a number of metrical characters in F_3, F_5, F_6, F_{13}, F_{15}, F_{18} and F_{19} generations. They found that both directional and stabilizing selection occurred for the characters studied and that variances generally decreased with advancing generations.

The progenies of a random sample of plants, selected from the population, were grown and between-family and within-family variances were estimated. For heading time and plant height the between-family variance was high in early generations and decreased steadily generation by generation indicating that

selection was against the more extreme families. However, the between-family variance in F_{19} was much larger than the within-family variance estimated on the original homozygous parents, and since the latter was an estimate of environmental variance, it was apparent that a great deal of genetic diversity, attributable to differences among families, still remained in the population. Measurements on the F_{39} generation of a similar barley population (CC II) indicated little if any further decrease in between-family variance. Apparently by the F_{19} generation, a balance had been reached between factors that increase and factors that decrease variability. It was also found that within-family variances for heading time and other metrical characters remained higher in the F_{19} generation than the average within-family variance of the original homozygous parents of the population. Again, little decrease was found in the F_{39} generation of CC II and this suggested that the individuals of which inbreeding populations are comprised are not fully homozygous and provide new variability each generation by segregation.

These results suggest that populations derived from hybrids rapidly reach an equilibrium in which loss of variability due to the combination of directional and stabilizing selection is balanced by steady release of new variability resulting from intercrosses

between individuals within the population. In this particular case the level of outcrossing was estimated to be approximately 1%.

Jain and Allard (1960) studied the number of seeds produced per individual in various generations of a composite cross population. There was a high proportion of individuals of very low fecundity in the early generations but the proportion of these declined sharply during the generations when yield was increasing rapidly. Thus the first stage in the evolution of such populations is the elimination of the unbalanced genotypes, leading to rapid improvement in mean population fitness. Continued evolution of the system appears to involve the slow approach to equilibrium.

An inbreeding population, particularly one created by a process of hybridization, is generally thought of as comprising a number of different, but true-breeding families. Allard and Jain (1962) suggest, however, that such families may be represented by only one individual. In other words, the great majority of individuals in a predominantly self-fertilizing population may, even if homozygous, be genetically unique.

There is evidence from studies of the fate of individual components of varietal mixtures that the best yielding varieties in pure stand do not always have good competitive ability in mixed stands (Allard,

1961; Harlan and Martini, 1938; Suneson and Wiebe, 1942). Suneson (1949) described an experiment in which four barley varieties were grown in mixture over many seasons and the variety Atlas dominated the population after sixteen years whilst the variety Vaughn was virtually eliminated. The varieties were not grossly different in growth, maturity or development but Vaughn had a better yield and greater resistance to leaf diseases when grown in pure stand than any of the other varieties and Atlas had the poorest leaf disease record and a mean yield below the medium for the component varieties. Such results sound a note of caution for the practise of allowing natural selection full rein in the development of composite cross populations where it is intended that pure line varieties shall be extracted from the genetically diverse populations. Suneson (1960) has emphasised the buffering effects of genetic diversity, particularly with regard to disease and pest resistance. Thus heterogeneous populations may foster the survival of disease-susceptible plants. Such weaknesses will become apparent when true-breeding families are selected from the populations.

Despite this reservation the setting up of composite cross populations provides a broad genetic base from which to work. Genetic variability is created by the low level of natural crossing, which

has been estimated at Pentlandfield to be about 2% (R.J.Giles, personal communication), and maintained perhaps by natural selection for heterozygous plants (Jain and Allard, 1960). Where a variety containing a gene for male sterility is deliberately incorporated, the level of genetic recombination will be very much increased. If grain for each new generation is harvested only from male-sterile plants, constant recombination can be expected and, provided sufficiently large populations can be grown, it might be expected that even fairly tight linkages might be broken thus releasing variability normally unavailable to the breeder.

APPENDIX III

BARLEY DIALLEL 1970

Field Diary and Observations

April 2	Fertilizer evenly spread over the area (50' x 70') by hand. 30lb of 20-10-10 were used giving 66.7 units of N. A bird-proof net was erected over the area.
May 19	Sowing into paper pots began.
May 26	First block completed.
May 28	First block and replacement sowings were watered.
May 29	Trial marked out, beds rotavated.
June 1	Guard-rows of Glacier sown using Planet drill. Soil dry.
June 3	Sowing completed. Second block watered.
June 9-10	Transplanting of first block.
June 12-14	Transplanting of second block.
June 14-15	Transplanting of replacement plants started.
June 15	Trial sprayed with insecticide.
June 16	Transplanting of replacement plants completed.
July 2-3	Trial scored for mildew.

July 6	Scoring of trial for time of heading began.
August 16-17	Heavy rain and strong winds caused rather severe lodging throughout the trial.
September 29-October 6	Trial harvested. Each plant uprooted and a label attached. Material hung up to dry in greenhouse.

NOTES

Presumably because of the late sowing, mildew attack was heavy and severly damaged some plants.

Bed 2A showed particularly poor growth at the west end of the bed, presumably due to poor soil. Plants were stunted, weak and late.

This trial was grown at Pentlandfield.

APPENDIX III

BARLEY DIALLEL 1971

Field Diary and Observations

April 5	Started sowing
April 20	Sowing of both blocks and replacement grains into paper pots completed and all watered together.
April 21	Guard-rows of Golden Promise sown into the field with Planet drill.
April 23	Rain.
May 10	Transplanted first block. Plants c 4" high. Weather conditions dry and windy.
May 11	Transplanted second block. Same weather conditions.
May 13	Watering by hand. Finished gap-filling and started planting remainder of replacement plants.
May 19	Net erected.
June 2	Trial top-dressed by hand with 20-10-10 fertilizer at a rate giving 60 units of N.
June 14	Scoring for time to heading began and labels attached to plants as they were scored.
June 22	Trial scored for mildew

June 23	Trial sprayed with Calixin.
July 2 and 5	Trial scored for mildew.
July 25-27	Rain every day.
September 7-10	Trial harvested. Plants hung up to dry in greenhouse.
September 13	Replacement plants harvested.

NOTES

Weather conditions throughout the planting period were extremely dry, sunny and windy. The plants seemed to stand up to these drying conditions surprisingly well.

Shortly after sowing and before erection of the net, some damage was caused by crows, apparently attracted by the aluminium labels. Missing plants were replaced and by June 2 the trial was looking very healthy.

As in the previous season, wet weather and wind shortly before the harvest caused lodging and some proliferation of back-tillers.

The trial was grown at The Murrays, Ford, Midlothian.

APPENDIX IV

THE DIALLEL CROSS

The method of diallel crossing was introduced by Schmidt (1919) as a means of comparing the breeding values of parents. When the parents are inbred lines, each can be crossed with every other, but if the parents are individuals this will only be possible if each can function as both male and female, otherwise the parents must be split into two groups. This sub-division, with crossing only between groups, is usually referred to by plant breeders as "test crossings".

There may be limitations in the genetic material or the experimental facilities which prevent the geneticist from making a complete set of crosses and in this case certain crosses can be omitted according to a design to give what is known as a <u>partial diallel cross</u> (Fyfe and Gilbert, 1963). The following account however deals only with the case where all possible crosses are made among the p parents, leading to p^2 matings. The cross is called the <u>complete diallel cross</u>. These p^2 combinations can be divided into three groups: 1) the p parental combinations $P_1 \times P_1$, $P_2 \times P_2$, ... $P_n \times P_n$; 2) one set of $\frac{1}{2}p(p-1)$ F_1 combinations; and 3) the set of $\frac{1}{2}p(p-1)$ reciprocal F_1 combinations. The parental inbreds and/or the reciprocal F_1's may or

may not be included so that four possible experimental situations can be distinguished: 1) parents, one set of F_1's and reciprocal F_1's are included (all p^2 combinations); 2) parents and one set of F_1's are included but reciprocal F_1's are not ($\frac{1}{2}p(p+1)$ combinations); 3) one set of F_1's and reciprocals are included but not the parents ($p(p-1)$ combinations); 4) one set of F_1's but neither parents nor reciprocals are included ($\frac{1}{2}p(p-1)$ combinations). There are two alternative sampling assumptions: 1) parental genotypes are assumed to be a random sample from some population about which inferences are to be made, or 2) the parental genotypes are deliberately chosen and cannot be regarded as a random sample from any population, that is, the experimental material constitutes the entire population about which inferences are to be made. (Griffing, 1956).

Most of the diallel cross analyses used in this work were developed by Jinks and Hayman (Jinks and Hayman,1953; Jinks, 1954; Hayman 1954a, 1954b). Griffing (1956) described eight different analyses for general and specific combining ability corresponding to the four experimental designs in each of the two sampling situations described above. One of these analyses was applied to the present data and is described below. Estimation of the components of genetic variation was done using an unweighted

least squares analysis (Mather, 1949) to solve a series of simultaneous equations relating a number of second degree statistics to the parameters for which estimates were required (Table AIV-1).

A detailed reiteration of the biometrical theory underlying these analyses would not be appropriate here and the purpose of this Appendix is to give sufficient information only for the interpretation of the analyses applied to the data from the diallel experiments conducted as part of this work.

Components of variation

Four genetic components can be estimated: D, which measures only additive effects, H_1 and H_2, which measure only dominance effects and which are identical when the frequencies of increasing and decreasing alleles are equal, and F, which can take sign. In the presence of unequal gene frequencies, the sign and magnitude of F can be used to determine the relative frequencies of dominant to recessive alleles in the parental population and the variation in the dominance level over loci. Thus F will be positive whenever the dominant alleles are more frequent than the recessive alleles, and negative when the reverse is true irrespective of whether the dominant alleles increase or decrease the expression of the character under study. The ratio $\frac{1}{2}F/\sqrt{[D(H_1-H_2)]}$ = 1 if the ratio of dominant effects

TABLE A IV - 1

Expectations in terms of genetical and environmental components

Generation	Statistic	Genetic expectation				Environmental expectation		
		D	F	H_1	H_2	E_o	E_1	E_2
	Vp	1	..	..	..	1/n		
F_1	$\bar{V}r$	$\frac{1}{4}$	$-\frac{1}{4}$	$\frac{1}{4}$	..	1/n	(n-1)/n	
	$V\bar{r}$	$\frac{1}{4}$	$-\frac{1}{4}$	$\frac{1}{4}$	$-\frac{1}{4}$	$1/n^2$	$(n-2)/n^2$	
	$\bar{W}r$	$\frac{1}{2}$	$-\frac{1}{4}$	..	..	1/n		
F_2	$\bar{V}r$	$\frac{1}{4}$	$-\frac{1}{8}$	$\frac{1}{16}$	..	1/n		(n-1)/n
	$V\bar{r}$	$\frac{1}{4}$	$-\frac{1}{8}$	$\frac{1}{16}$	$-\frac{1}{16}$	$1/n^2$		$(n-2)/n^2$
	$\bar{W}r$	$\frac{1}{2}$	$-\frac{1}{8}$	..	..	1/n		
F_1 and F_2	$\bar{W}r_{12}$	$\frac{1}{4}$	$-\frac{3}{16}$	$\frac{1}{8}$	..	1/n		
	$W\bar{r}_{12}$	$\frac{1}{4}$	$-\frac{3}{16}$	$\frac{1}{8}$	$-\frac{1}{8}$	$1/n^2$		
	E_o					1		
	E_1						1	
	E_2							1

Cont'd...

TABLE A IV - 1 continued

Vp is the variance of the parent lines.

$\bar{V}r$ is the mean variance of arrays

$V\bar{r}$ is the variance of array means.

$\bar{W}r$ is the mean parent-offspring covariance for members of the same array.

$\bar{W}r_{12}$ is the mean of the covariances of F_1 and F_2 in each array.

$W\bar{r}_{12}$ is the covariance of the array means of the F_1 and F_2 generations.

E_o, E_1 and E_2 are the direct measurements of environmental variance for the parental F_1 and F_2 generations respectively.

An array is a parent and all the crosses involving that parent.

and additive effects is constant over all loci. However, if the additive and dominance effects of genes vary independently over loci, this ratio will have a value of zero. The ratio of the total numbers of dominant to recessive genes in all the parents is found from $(4DH_1)^{\frac{1}{2}} + F/(4DH_1)^{\frac{1}{2}} - F$. An overall measure of dominance is given by the ratio $(H_1/D)^{\frac{1}{2}}$, where a value of more than 1 indicates over-dominance, a value of 1 indicates complete dominance, and a value of less than 1 indicates partial or incomplete dominance.

The ratio $\frac{1}{4}H_2$ to H_1 or $H_2/4H_1$ measures the average value of $\underline{uv}$ over all loci, where $\underline{u}$ is the frequency of increasing alleles and $\underline{v}$ $(=1-\underline{u})$ is the frequency of decreasing alleles. Where $\underline{u} = \underline{v} = \frac{1}{2}$ at all loci, $\underline{uv} = 0.25$.

The estimates of the genetic components obtained from the least squares analysis can be used to reconstruct the values which they would lead us to expect for the statistics. The deviations of these expectations from the observed values can then be obtained and the sum of squares of these deviations is a measure of the adequacy of the genetic components to account for the variation observed. It also can be used to find the standard errors of the components if there are more equations than unknowns in the analysis, but the estimation of $\underline{n}$ parameters from $\underline{n}$ statistics leads to a perfect fit solution and the

precision of the estimates cannot be tested.

The W/V graphical analysis

The graphical analysis described by Jinks (1954) and Hayman (1954a), depends upon the relations between Vr, the variance of all the offspring of the r^{th} parent, and Wr, the covariance between these offspring and their non-recurrent parents, environmental variance being neglected. Extended to an arbitrary number of independent genes, $Wr - Vr = \frac{1}{4}D - \frac{1}{4}H_1$. In the regression form, $y = a + bx$, this can be expressed as $Wr = \frac{1}{4}(D - H_1) + bVr$ where $b = 1$. When $Vr = 0$, $Wr = \frac{1}{4}(D - H_1)$ so that on the Wr,Vr graph the Wr intercept is an indicator of the average degree of dominance in the experimental material. The distance of the intercept from the origin is $\frac{1}{4}(D - H_1)$ so that $D > H_1$ when the intercept is positive (incomplete dominance), $D = H_1$ where the line passes through the origin (complete dominance), and $D < H_1$ when the intercept is negative (over-dominance). These conclusions, which depend upon the position of the line relative to the axis, hold only for the genetic component of the Wr and Vr values. Correction for the environmental components of the mean values for Wr and Vr allows a true estimate of the relative values of D and H_1 to be made. Where there is no dominance ($H_1 = 0$), all the points cluster at a single point where $Wr = 2Vr$ as

$$Vr = \tfrac{1}{4}D = \tfrac{1}{4}Vp$$

$$Wr = \tfrac{1}{2}D = \tfrac{1}{2}Vp$$

where Vp is the variance of the parent lines, and there is no regression.

The positions of the array points along the regression line depend on the relative proportions of of dominant and recessive genes among the parents. For a single gene the effect of dominance will be to make the heterozygote of the gene identical in phenotype to the dominant homozygote. Thus parents containing the greatest number of dominant homozygotes for the genes controlling the character in question will show the least variation amongst themselves (Vr) and the least covariance with their other parents (Wr). Points representing arrays of these parents will lie close to the origin on the Wr,Vr regression whilst, at the other extreme, points representing arrays of recessive parents will lie furthest away from the origin.

A limiting parabola, defined by $Wr^2=VrVp$ can be superimposed on the Wr,Vr graph and will cut the regression line at two points representing the positions corresponding to varieties carrying the full complement of dominant or recessive genes.

A failure of the model, that is, of the basic hypotheses upon which the analysis is based (see Hayman, 1954a), will be indicated by a departure of

the regression slope from unity. The failure may be due either to epistasis (non-independent action of non-allelic genes), or to correlated gene distributions (non-independent distribution between parents). A scaling test may confirm the presence of epistasis.

A further relationship between the statistics derivable from a diallel set of crosses is that between Wr and W'r, the covariance of array members with the array means of their non-recurrent parents. Since W'r tends towards lower values for dominant parents and higher values for recessive parents, the W'r, Wr regression may be used to detect the order of dominance in the same way as the Wr,Vr graph. Further, when the distributions of negative and positive alleles (for genes with dominance effects) are equal, the slope of the regression line will be one half and pass through the origin. Deviation from a slope of one half indicates asymmetrical gene distribution and in this case parents with common genotypes will fall above the line of slope one half whereas parents with different or relatively rare genotypes will fall below this line.

Analysis of variance of diallel tables

In a diallel set of crosses the total variation among the progeny family means can be attributed to differences among maternal parents, differences among paternal parents and the interaction between them.

These are the standard items of an analysis of variance of a table in which differences between row totals, column totals and their interaction can be recognised. In a diallel table however, reciprocal crosses have identical expectations and for the simple additive-dominance model, apart from sampling variation, the two halves of the table about the leading diagonal should be mirror images of each other.

The general requirements of any analysis of variance of a diallel table are that it provides appropriate tests of the additive and non-additive effects, irrespective of whether there are reciprocal differences among progeny families, and provides a test for the presence of the latter (Mather and Jinks, 1971). Such an analysis was described by Hayman (1954b) and is similar to that given by Yates (1947). The main items which can be tested in the Hayman analysis are:

a variation between the mean effects of each parental line - (additive effects),

b variation in the reciprocal sums not ascribeable to a - (non-additive effects),

c average maternal effects of each parental line,

d variation in the reciprocal differences not ascribeable to c.

The b item is sub-divided into b_1, b_2 and b_3. The b_1 item tests the mean deviation of the F_1's from

their mid-parental values. It is significant only if there is a directional dominance effect. The $\underline{b}_2$ item tests whether the mean dominance deviation of the F_1's from their mid-parental values within each array differs over arrays. It will do so if some parents contain considerably more dominant alleles than others. The $\underline{b}_3$ item tests that part of the dominance deviation that is unique to each F_1 and is analagous to the specific combining ability in Griffing's Method 3 analysis.

When reciprocal effects are not significant the $\underline{c}$ and $\underline{d}$ items and the block interactions are all estimates of the environmental component of variation. If genotype x environment interactions are present they will be detected as differences between the block interactions with each main effect. Generally each main effect is tested against its own interaction with environment. However if the six interaction terms can be shown by a Bartlett's test to be homogeneous they may be pooled to give a common error variance (Bt). In the work described here the average within-family variance for F_1 and parents was considered the best estimate of the environmental component of variation and was used where possible to test the main effects and the interactions in the Hayman analysis.

In cases where reciprocal differences are presumed absent or where practical considerations make it difficult to make large numbers of hybridizations,

diallel sets may be produced where only one of each pair of reciprocal crosses is raised. The appropriate analysis, based on that described by Hayman, is given by Jones (1965). The form of the analysis is the same as that given above except that sums of squares corresponding to c and d cannot of course be computed.

The analysis of variance proposed by Griffing (1956) essentially estimates combining ability, both general and specific. These estimates are equivalent to additive and non-additive components. The analysis tests the mean squares for general and specific combining ability against residual error and the effects themselves can be estimated from the formulae appropriate to the particular method and model to which the data correspond. Although the parental lines were grown in the diallel experiments described here, they were not included in the data for the combining ability analyses in order not to bias the estimates (Griffing, 1956). The analysis described under Method 4 was therefore used.

APPENDIX V

CANONICAL VARIATE ANALYSIS

As a starting point for a multivariate study the data can be conveniently represented in the form of a data matrix ($\underline{X}$) having $\underline{n}$ rows and $\underline{p}$ columns, so that the number $\underline{x}_{ij}$ in the $\underline{i}^{th}$ row and the $\underline{j}^{th}$ column of this matrix gives the value of the $\underline{j}^{th}$ variate for the $\underline{i}^{th}$ unit.

$$\underline{X} = \begin{bmatrix} x_{11} & x_{12} & \cdots\cdots & x_{1p} \\ x_{21} & x_{22} & \cdots\cdots & x_{2p} \\ \vdots & \vdots & & \vdots \\ x_{n1} & x_{n2} & \cdots\cdots & x_{np} \end{bmatrix}$$

A measure of the relationship between any two variates can be obtained from the matrix $\underline{X}'\underline{X}$, where $\underline{X}'$ is the transpose of $\underline{X}$. The $\underline{i}^{th}$ diagonal element of this matrix contains the sum of squares of the components of the $\underline{i}^{th}$ variate, and the element in the $\underline{i}^{th}$ row and the $\underline{j}^{th}$ column when $\underline{i} \neq \underline{j}$) contains the sum of products of corresponding components for the $\underline{i}^{th}$ and $\underline{j}^{th}$ variates. Thus $\underline{X}'\underline{X}$ is termed the sum of squares and products (SSP) matrix. Variances and covariances may then be estimated from $(1/(n-1))\ \underline{X}'\underline{X}$.

The data matrix $\underline{X}$ readily lends itself to a geometrical representation where each unit is treated as a point in $\underline{p}$ - dimensional space with the value of the $\underline{j}^{th}$ variate represented on the $\underline{j}^{th}$ of $\underline{p}$ rectangular axes. Thus the sample of $\underline{n}$ units is represented as a scatter of $\underline{n}$ points in $\underline{p}$ - dimensional space. When $\underline{p}$ is large such a model may be difficult to interpret and the reduction of dimensionality may be important as the first stage of the analysis (Krzanowski, 1972). A number of techniques is available for the effective reduction of dimensionality and among these is the canonical variate analysis.

The application of this analysis supposes a data matrix upon which a structure has been imposed. This consists in the division of the rows of the matrix into $\underline{h}$ groups, each group representing a distinct population. The purpose is to represent the data in as few dimensions as possible and in a manner which will maximize the discrimination between the groups. The matrix $\underline{X}'\underline{X}$ can in this case be split into two components: $\underline{B}$ which is the SSP matrix between groups and $\underline{W}$, the SSP matrix pooled within groups.

The latent roots or eigenvalues (λ) of $\underline{W}^{-1}\underline{B}$, where $\underline{W}^{-1}$ is the inverse of the matrix $\underline{W}$, are defined by the determinantal equation.

$$\left|\underline{W}^{-1}\underline{B} - \lambda\underline{I}\right| = 0$$

and the corresponding eigenvectors are determined by

equations of the set

$$(\underline{B} - \lambda\underline{W})\ \underline{l} = 0,$$

where $\underline{l}$ is a $\underline{p}$-component vector with the last component set equal to unity. For each of these vectors the normalized equivalent is computed such that the within-group variance of a canonical variate is unity. The first axis accounts for the maximum possible variance of the data. The second axis is perpendicular to the first and accounts for as much as possible of the remaining variance, and so on. This is referred to as a rotation of the axes and is an example of a linear transformation. Thus if a point, representing the mean of the $\underline{i}^{th}$ group, has co-ordinates x_1, ..., $\underline{x}_p$ on the original axes, each of its new co-ordinates will be a weighted sum of the $\underline{x}$'s. In the derivation of the co-ordinates on the j^{th} canonical axis the weightings are given by the elements of the vector $\underline{l}_j$ according to the linear equation

$$y_{ij} = l_{j1}x_1 + l_{j2}x_2 + ... + l_{jp}x_p.$$

If there are more variables ($\underline{p}$) than groups ($\underline{h}$) and in particular if $\underline{p} > \underline{h} - 1$, there will be only $\underline{h} - 1$ non-zero latent roots. If $\underline{p} < \underline{h} - 1$ there will be $\underline{p}$ latent roots. Further details of the analysis are given by Seal (1964) and Hope (1968).

One of the assumptions upon which the analysis rests is that the distribution of members of a population about the population mean is multivariate

normal. By joining together areas of equal density we should obtain an ellipsoidal surface whose centroid is the population mean. Every sample may therefore be represented as an ellipse or, if $p > 2$, an ellipsoid. It is a further assumption that these ellipsoids do not differ significantly from one another (see Reyment, 1969). However the test for homogeneity of dispersions is often omitted (Hope,1968) since it is sensitive also to departures from normality and a significant chi-square may indicate either that the dispersions are heterogeneous or that distributions are non-normal. In fact the canonical analysis is fairly robust even to quite considerable deviations from homogeneity.

The nature of the transformation which results from the canonical analysis may be grasped by imagining two axes (representing two measured variates) at right angles to each other, and two samples, plotted relative to the axes, represented by 2-dimensional elliptical swarms. Then the shapes and orientations of these two samples will be determined by the correlation between the two axes. If the axes are now rotated and rescaled until the two ellipses become circles, the rotation will be through the angle whose cosine corresponds to the correlation between the two variates. With more than two axes considered, ellipsoids are transformed to spheres

and the radius of a sphere is the standard deviation within samples. The distance between the centres of any two spheres is Mahalanobis' D for the two groups.

Diallel Analysis of the Time To Heading in Spring Barley

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1. Introduction

Reviews of the published studies on time to heading in barley have been compiled by Smith (1951) and Nilan (1964). Early genetic studies were generally limited to single or a small number of crosses and the results indicated variously that the character was simply or polygenically determined and that dominance was present in varying degrees. Later studies, using more sophisticated statistical techniques, have also led to the conclusion that the character is quantitatively inherited and that it is partially governed by dominant genes or gene groups.

Johnson and Paul (1958) analysed data from the F_1, F_2 and F_3 generations of seven crosses between spring barley varieties of different maturity periods and concluded that additive alleles at two loci were operative in the inheritance of earliness. These authors rejected the biometrical technique of analysis proposed by Mather (1949) in favour of Mendelian analysis. Eunus (1964) re-analysed the data from five of the seven crosses by biometrical techniques and concluded that two to five effective factors were operating. He also detected overdominance in three of the five crosses. Aksel and Johnson (1961) studied " sowing-to-heading period " in 10-parent (six-rowed and two-rowed varieties) and 6-parent (six-rowed varieties) diallels at F_2. Biometrical analyses described by Hayman (1954*b*) were used and the 6-parent crosses were also analysed by a single array technique (Jinks, 1956). They found that dominance acted in the direction of short sowing-to-heading period and that the two-rowed varieties fell in the most recessive group. Of the six-rowed varieties, O.A.C. 21 was one of those showing an excess of recessive genes.

The results of Paroda and Hayes (1971) confirmed previous findings, that the character was quantitatively inherited and that both additive and dominance components were present. They found a considerable shift in the position of relative dominance of different arrays in different environments and stressed the need to carry out genetic studies in environments similar to those in which the information is to be applied.

The results to be described here were obtained for two seasons from a 13-parent diallel in which parents, F_1 and F_1 were grown in the same experiment.

2. Materials and methods

The experiment* was conducted in order to study a number of quantitatively inherited agronomic characters including yield and its components and

* After the completion of this experiment the original Deba Abed stock was found to be heterogeneous for rachilla hair length. No obvious morphological heterogeneity was apparent during the course of the crossing programme.

TABLE 1

List of parents, pedigree and source of origin of parents used in the diallel

Variety	Origin	
1. Olli*	Selection from a Finnish variety	Ottawa, Canada
2. Pirkka*	(Maskin × Finnish variety) × (Olli × Manchurian variety)	Tammisto, Finland
3. Cambrinus	Balder × Strengs Franken III	Groningen, Holland
4. Ymer	Maja × (Seger × Opal)	Svalov, Sweden
5. Deba Abed	Abed Denso × Wihenstephaner II	Abed P.B.S., Denmark
6. Scotch Bere*	Old Scottish land race	Scotland
7. O.A.C. 21*	Selection from Mandscheuri barley	Ontario, Canada
8. Golden Promise	Gamma-ray mutant from Maythorpe	D. Miln & Co., Chester, England
9. Maris Baldric	Spratt Archer × Freja	P.B.I., Cambridge, England
10. Midas	((Proctor × Wong) × Mildew resistant "A") × Gamma-ray mutant from Maythorpe	D. Miln & Co., Chester, England
11. Mosane	Balder × Piroline	Gembloux, Belgium
12. Sultan	((((Kenia × Arabian) × Kenia) × F_1 Agio) × Kenia) × Balder	CEBECO, Holland
13. Boreham Warrior	Plumage Archer × Freja	Guinness, Warminster, England

* Six-rowed varieties.

the production of diastatic enzymes. The 13 spring barley varieties used in the study are listed in table 1. Most of the two-rowed varieties are currently of some commercial interest, whilst the six-rowed varieties, with the exception of Scotch Bere, were chosen for their high diastatic enzyme activity during germination. Scotch Bere was included as an adapted six-rowed variety which had not been subjected to selection for diastatic power.

Data are presented here for time to heading in the material grown, though the varieties were not chosen primarily for the study of this character. They do, however, represent a fairly wide range (table 2).

TABLE 2

Mean number of days to heading for parents relative to Boreham Warrior

	1970		1971	
Variety	I	II	I	II
1	−17·3	−16·4	−14·2	−17·7
2	−12·7	−10·6	−9·7	−9·9
3	−6·4	−6·3	−4·6	−7·2
4	−6·3	−5·1	−4·5	−4·3
5	−6·9	−5·3	−4·6	−7·6
6	−6·5	−4·8	−5·0	−6·2
7	−12·1	−10·5	−6·5	−11·1
8	−6·0	−1·7	−4·8	−4·1
9	−8·7	−5·2	−1·9	−4·9
10	−4·0	−2·5	+2·0	−2·3
11	−6·5	−5·4	−4·8	−6·2
12	−3·4	−1·6	−2·6	−3·1
13	0·0	0·0	0·0	0·0

Hybrid material was produced by hand-pollination in the greenhouse during 1968 and 1969. Whenever possible, 30 grains of each F_1 hybrid were produced. Seed of the F_2 generation was obtained by selfing four F_1 plants of each cross in the greenhouse.

The experiment consisted of genotypes 1 to 9 (table 1) crossed in a full diallel (including parents and reciprocals) of five sibs per cross per replicate; a 13×13 half diallel (not including reciprocals and comprised partly of the pooled reciprocal crosses from the 9×9 full-diallel set), with ten sibs per cross, and a 13×13 F_2 half diallel, again with ten sibs per cross. Ten plants of each parent were also included and, in the case of the F_1 full diallel, five plants were sampled from ten to represent the parents. Two replicate blocks were sown in each of two years and plants were individually randomised within each replicate.

Seeds were sown in paper pots (" Japanese Plant Pots ") which were 2 cm. diameter by 12·5 cm. long. Sowing was done according to the field plan and dry soil was used so that the whole experiment could be watered at the same time on completion of sowing. In addition to the experimental material, five spare grains of each genotype were sown to replace losses.

Seedlings approximately 10 cm. tall were transplanted into dibbed holes in rows set 15 cm. apart, with 7·5 cm. between plants within rows. Each replicate consisted of two sub-blocks, of four rows each, surrounded by two guard-rows.

Time to heading was recorded for each plant as the number of days from an arbitary date to the day when 2-3 cm. of awn were visible above the auricle of the flag leaf on the main tiller.

Computer programs were written to perform the analyses of Jinks and Hayman (1953), Hayman (1954*a*, *b*), Jinks (1954) and Jones (1965), and for the least squares estimation of genetic components. The programs were used on the IBM 360/50 and ICL System 4/75 computers of the Edinburgh Regional Computing Centre.

3. Results

Variances were calculated for each cross and tested for homogeneity using Bartlett's Test. Significant heterogeneity was detected in the 1970 data which was only partly accounted for by correlations between means and variances. Logarithm and square-root transformations did not appreciably reduce this heterogeneity and all subsequent analysis was conducted on the untransformed data. Heterogeneity of variance was also detected in the 1971 data and no correlation was found between means and variances. Again, all analyses were conducted on untransformed data.

Table 2 shows the range, represented by the parents, of the character under consideration. Boreham Warrior was the latest parent except in replicate block I in 1971, where Midas was 2·0 days later. The four sets of comparative times of heading, with this exception, show considerable consistency.

Analyses of variance using the model proposed by Hayman (1954*a*) are shown in table 3 (*a*) for the full-diallel sets and in table 3 (*b*) for the half-diallel sets. The method for the analysis of half-diallel tables is described by Jones (1965). Additive and non-additive effects were evident in all the analyses but there was no indication of significant reciprocal effects in the

TABLE 3 (*a*)

Analysis of data for time to heading in each of two seasons

Item	d.f.	9 × 9 F_1 1970 M.S.	9 × 9 F_1 1971 M.S.
a	8	1188·66***	1090·17***
b_1	1	21·16	15·36
b_2	8	27·85*	16·51
b_3	27	38·46***	26·30***
b	36	35·62***	23·82***
c	8	19·31	20·69
d	28	18·09	9·64
Blocks	1	4·71	108·53**
Ba	8	25·22*	12·88
Bb_1	1	0·98	5·54
Bb_2	8	2·39	15·56
Bb_3	27	16·25	11·50
Bb	36	12·74	12·24
Bc	8	13·82	11·95
Bd	28	13·22	16·64
Bt	80	14·27	13·81
Within-family variance		12·47 (645 d.f.)	11·36 (646 d.f.)

TABLE 3 (*b*)

Analysis of data for time to heading in each of two seasons

Item	d.f.	13 × 13 F_1 1970 M.S.	13 × 13 F_1 1971 M.S.	13 × 13 F_2 1970 M.S.	13 × 13 F_2 1971 M.S.
a	12	2226·28***	2037·97***	2754·96***	1630·29***
b_1	1	26·07	100·28**	795·85***	1032·14***
b_2	12	86·12***	44·42***	116·04***	26·77**
b_3	65	45·35***	34·32***	35·90***	24·18***
b	78	51·38***	36·72***	57·97***	37·50***
Blocks	1	5·12	217·92***	498·32***	732·70***
Ba	12	21·33	15·26	11·09	16·08
Bb_1	1	0·21	12·88	74·73*	2·06
Bb_2	12	5·56	11·47	9·75	8·62
Bb_3	65	12·84	11·25	30·49***	16·72**
Bb	78	11·56	11·30	27·86***	15·29*
Bt	90	12·86	11·83	25·63***	15·39*
Within-family variance (F_1 + Parents)		13·14 (1631 d.f.)	11·46 (1635 d.f.)		

*** Probability < 0·001 ** Probability 00·01 – 0·01 * Probability 0·01 – 0·05

analyses of the full-diallel sets (table 3 (*a*)). In all cases the main effects were tested against the within-family variance as being the best measure of environment. In most cases this item was close in value to the block × genotype interaction item, *Bt*.

Additive gene effects are clearly involved in the inheritance of this character, but non-additive effects are also important.

For each diallel table the variance (*Vr*) and parent-offspring covariance (*Wr*) of members of the same array were calculated and the regression of *Wr* on *Vr* was performed. Since the analyses of table 3 (*a*) gave no evidence of reciprocal effects, attention was confined mainly to the 13 × 13 half-diallel sets.

1970 Data

Analysis of the form described by Mather and Jinks (1971) was performed in which the differences in the magnitude of $Wr-Vr$ and $Wr+Vr$ over arrays were tested with the differences over replicate blocks. Highly significant differences in $Wr+Vr$ values over arrays were revealed in the F_1, indicating non-additive genetic variation. Significant differences between $Wr-Vr$ values indicated that the simple model was inadequate. Examination of the $Wr-Vr$ values revealed clear and consistent deviations, over replicate blocks, associated with arrays 4, 7 and 10. When the C-scaling test (Mather, 1949) was applied, interaction was evident for 13 crosses common to both replicate blocks. However, when the regression of Wr on Vr was plotted for means over blocks, the rather poor linear fit ($b = 0{\cdot}4924 \pm 0{\cdot}1032$) appeared to be due mainly to the point representing the Midas array (10) and re-analysis, with data for Midas omitted, gave $b = 0{\cdot}7748 \pm 0{\cdot}0513$ with no significant heterogeneity for values of $Wr-Vr$. Omission of both the Midas (10) and O.A.C. 21 (7) arrays from the analysis gave a regression $b = 0{\cdot}8329 \pm 0{\cdot}0441$.

After omitting only the Midas array the regression coefficients b, Wr/Vr for each block were compared in a joint regression analysis. The joint regression was highly significant and the replicate blocks were in agreement. Fig. 1*a* shows the Wr, Vr graph for the diallel table of means over replicate blocks. The graph indicated partial dominance with array 1 (Olli) containing most of the dominant genes and array 7 (O.A.C. 21) containing most of the recessive genes. The regression coefficient differed significantly from 1, indicating non-allelic interaction or correlated gene distributions. No correlation was found between yr, the mean of the common parent, and $Wr+Vr$, indicating that dominance was not unidirectional. The Wr, Vr graph for the F_2 data is shown in fig. 1*b*. The slopes of the regression lines were similar in both graphs and the Olli array clearly contains far more dominance than any of the other arrays.

Regression of Wr on Vr for the 4×4 six-rowed diallel gave coefficients for both blocks not significantly different from 1, and the joint regression coefficient was $0{\cdot}9762 \pm 0{\cdot}0733$. The Wr, Vr graph for mean values over blocks is shown in fig. 2*a*. The intercept of the regression line on the Wr axis indicated partial dominance and the Olli array again occupied a position nearest the origin but the locally adapted variety, Scotch Bere, now occupied the extreme recessive position. A high correlation ($r = 0{\cdot}9308$) was found for $Wr+Vr$ and yr, indicating that dominance was acting in the direction of earliness. Analysis of variance for the half-diallel table confirmed both additive and non-additive effects.

Considering now the two-rowed population, analysis of variance for $Wr+Vr$ and for $Wr-Vr$ over arrays and blocks revealed no significant differences and although the joint regression analysis for b Wr/Vr failed to indicate heterogeneity of regression between the two blocks, the regression for block I was not significantly different from zero whilst that for block II was just significant ($P < 0{\cdot}05$). The Wr, Vr graph for mean values over blocks showed apparent over-dominance which was no doubt a spurious result of interaction. Again, removal of the Midas array resulted in a regression line with a slope not differing from unity and passing through the origin of the Wr and Vr axes (fig. 3*a*). Complete dominance was thus

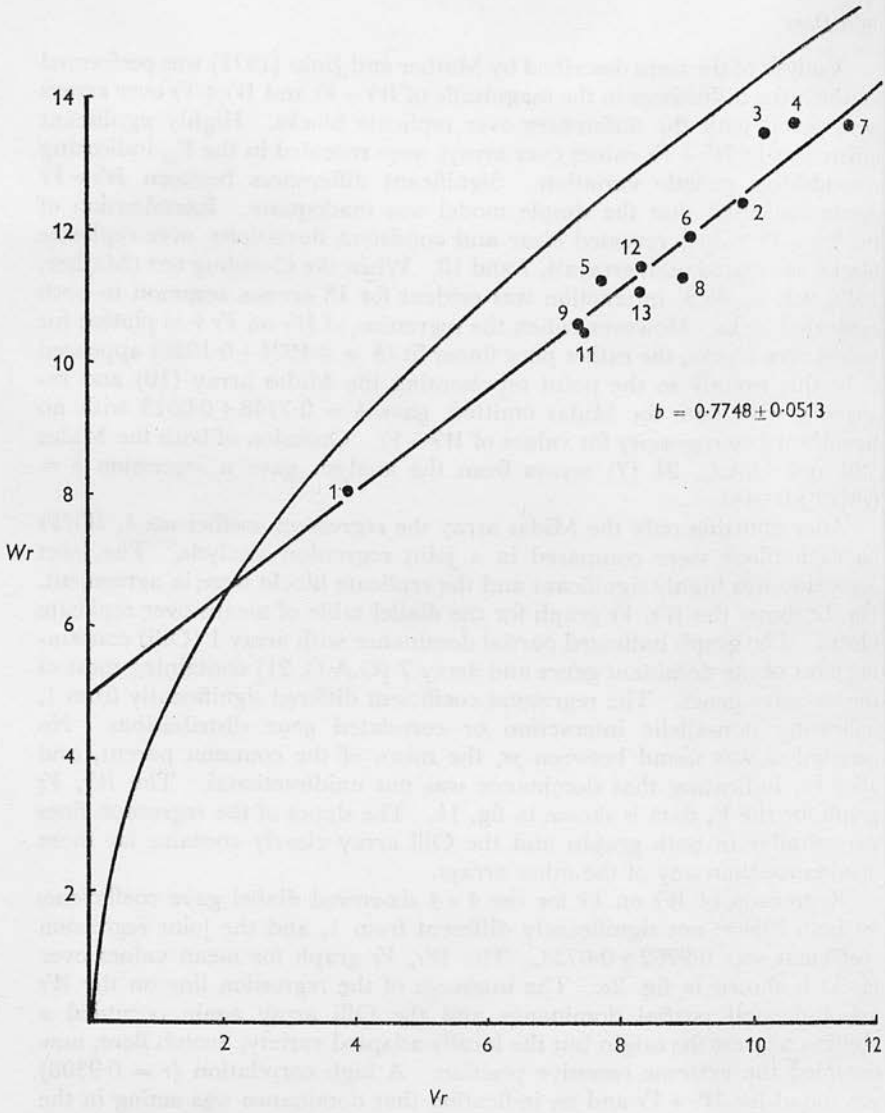

FIG. 1*a*.—*Wr*, *Vr* graph for the 13 × 13 F_1 half-diallel set, means over blocks, 1970 data, omitting data for array 10.

indicated with the Deba Abed array (5) containing the most dominant genes, a position, relative to the other two-rowed varieties, which was not apparent when data from the six-rowed population was included in the analysis (fig. 1*a*). No simple relationship was found between position on the regression line and parental phenotype performance. The correlation coefficient for $Wr + Vr$ and yr was $r = 0{\cdot}2183$, which did not reach significance.

The orders of dominance for arrays in both the six-rowed and two-rowed populations were confirmed when $W'r$ was plotted against Wr. The dotted lines in figs. 2*b* and 3*b* represent slopes of $\frac{1}{2}$ passing through the origin. In

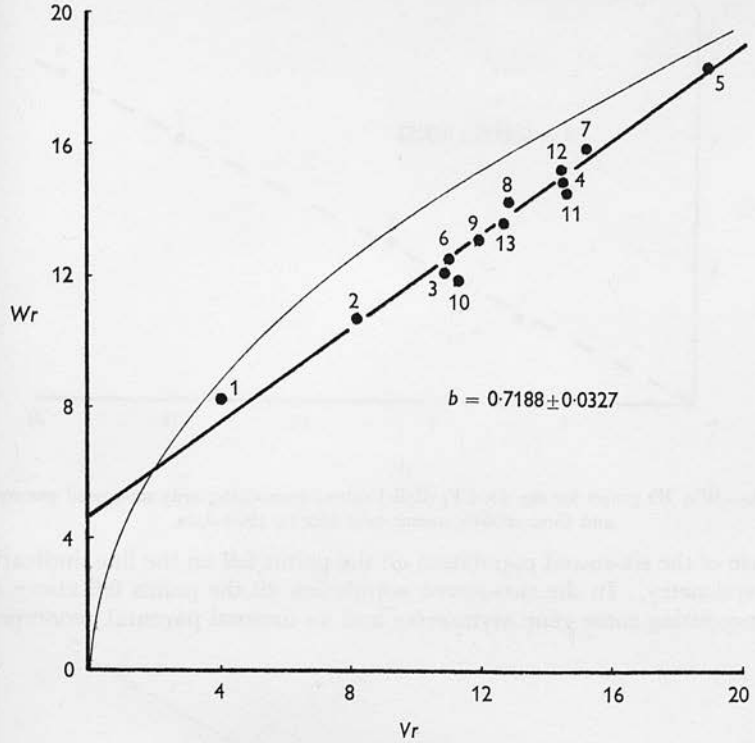

FIG. 1*b*.—*Wr*, *Vr* graph for the 13 × 13 F_2 half-diallel set, means over blocks, 1970 data.

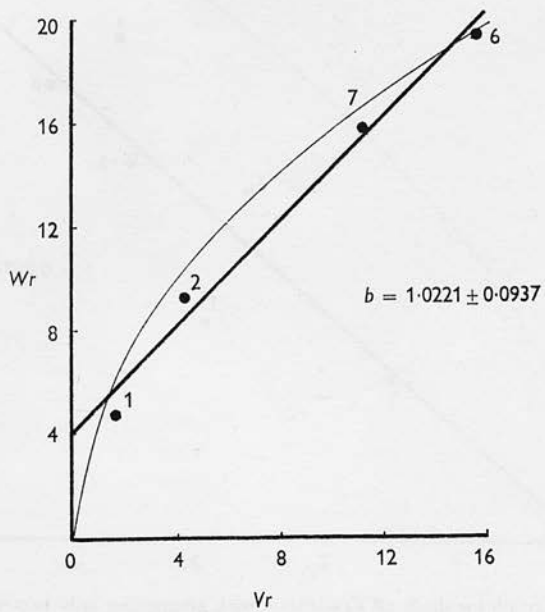

FIG. 2*a*.—*Wr*, *Vr* graph for the 4 × 4 F_1 diallel subset, comprising only six-rowed genotypes and their crosses, means over blocks, 1970 data.

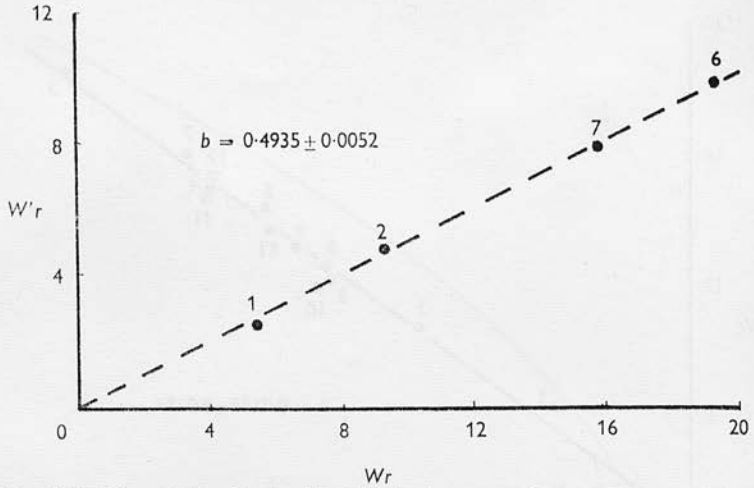

FIG. 2*b*.—*W'r*, *Wr* graph for the 4 × 4 F_1 diallel subset comprising only six-rowed genotypes and their crosses, means over blocks, 1970 data.

the case of the six-rowed population all the points fell on the line, indicating gene symmetry. In the two-rowed population all the points fell above the line, suggesting some gene asymmetry and no unusual parental genotypes.

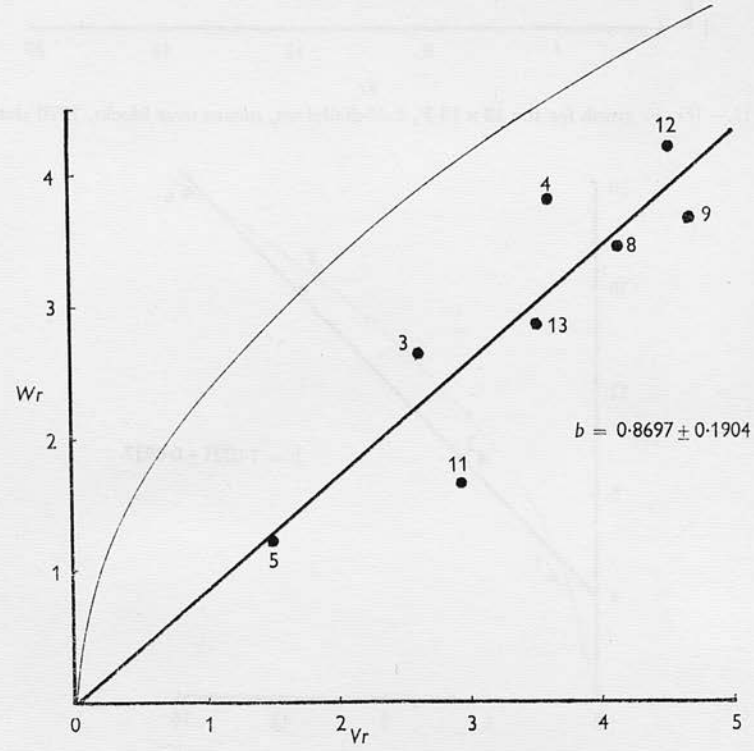

FIG. 3*a*.—*Wr*, *Vr* graph for the 8 × 8 F_1 diallel subset, comprising only two-rowed genotypes and their crosses and omitting the interacting Midas array, means over blocks, 1970 data.

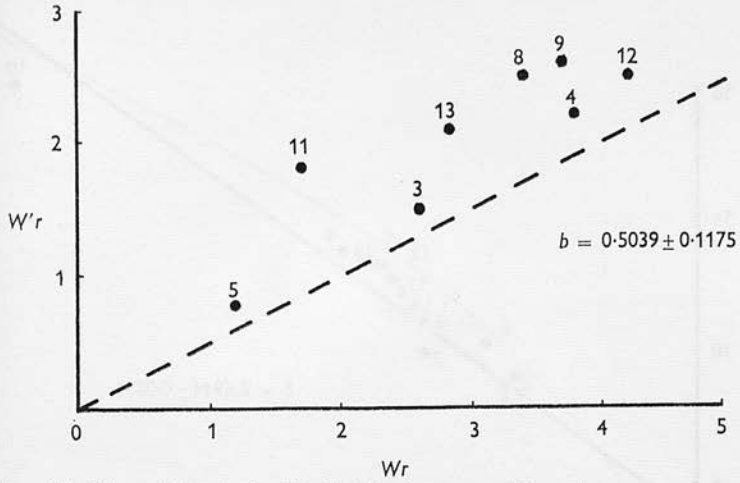

FIG. 3*b*.—*W'r*, *Wr* graph for the 8 × 8 F_1 diallel subset, comprising only two-rowed genotypes and their crosses and omitting the interacting Midas array, means over blocks, 1970 data.

1971 Data

Wr, *Vr* graphs for the 13 × 13 F_1 and F_2 diallel sets are shown in figs. 4*a* and 4*b*. In the F_1 generation the Olli array again occupied the position of the most dominance, and partial dominance was indicated for the population as a whole. In both replicate blocks the Midas array occupied a position of high variance and covariance, but the value of $W_{10} - V_{10}$ was large and negative when all other values were positive. Apparently the Midas array was again showing interaction and depressing the slope of the regression The C-scaling test showed interaction in four crosses with Midas in replicate block 2 but no Midas crosses showed interaction in block 1.

When the F_1 data, after omitting the Midas array, were re-analysed, a slope not differing from 1 was obtained. A correlation was found between *yr* and $Wr + Vr$ ($r = 0{\cdot}8036$, $P < 0{\cdot}01$) showing that dominance was acting in the direction of earliness.

When the six-rowed and two-rowed populations were analysed separately, the six-rowed population again showed a very good fit to a regression of unit slope (joint regression coefficient $b = 0{\cdot}9481 \pm 0{\cdot}0556$). The Olli and Pirkka arrays showed more dominance than the O.A.C. 21 and Scotch Bere arrays which alternated in the two blocks for the extreme position for recessive genes. The two-rowed population gave regression coefficients which differed markedly between replicate blocks ($b = 0{\cdot}7916 \pm 0{\cdot}2042$ and $b = 0{\cdot}1879 \pm 0{\cdot}0557$) and removal of the Midas array resulted in a non-significant regression for block 1 and a slope significantly less than 1 in block 2.

For the estimation of the six components of variation, *viz*. D, H_1, H_2, F, E_0, E_1 (or E_2 for F_2 generation) six statistics were available in F_1 and F_2. These were the variances of the parents (Vp), mean variances of arrays ($\bar{V}r$), variances of array means ($V\bar{r}$), mean covariances of arrays ($\bar{W}r$) and the direct estimates of environmental variances E_0, E_1 and E_2 for the parental, F_1 and F_2 generations respectively.

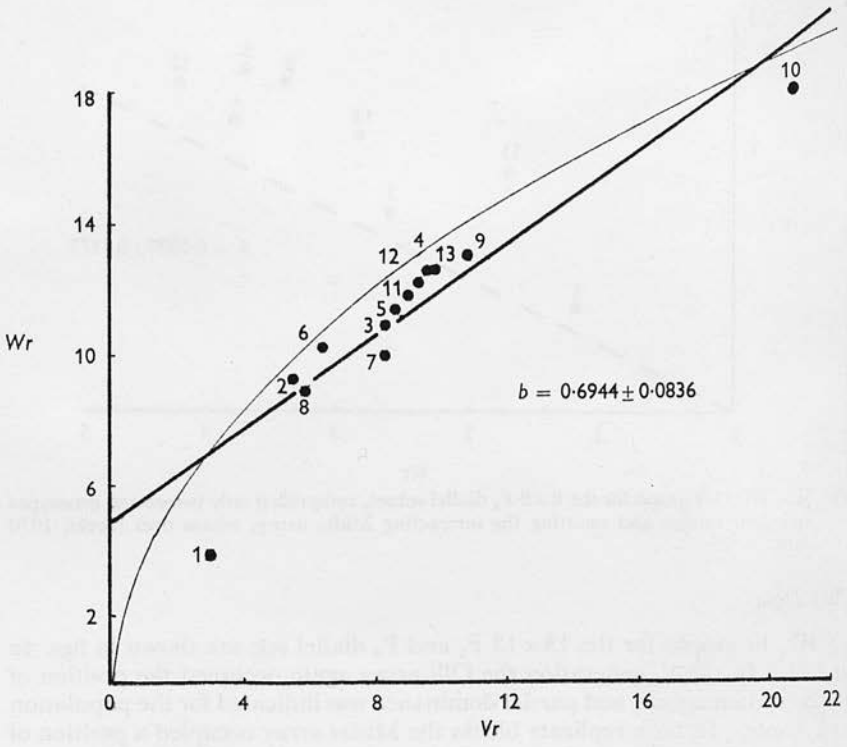

FIG. 4*a*.—*Wr*, *Vr* graph for the 13 × 13 F_1 half-diallel set, means over blocks, 1971 data.

The six equations were solved by an unweighted least squares technique (Mather, 1949; Mather and Vines, 1952; Mather and Jinks, 1971). The estimation of six parameters from six statistics in each generation resulted in a perfect solution and no standard errors could be attached to the values obtained. Values for the components and ratios between them are given in table 4 for F_1 and F_2 in each season.

The existence of partial dominance is confirmed by $\sqrt{(H_1/D)} < 1$ in almost all cases, though the very high estimates obtained for H_1 and H_2 in F_2 for both replicate blocks in 1970 and one replicate block in 1971 resulted in $\sqrt{(H_1/D)} > 1$, indicating over-dominance, which was not suggested by the *Wr*, *Vr* graphs.

The negative value of F suggests that there was an excess of recessive alleles present in the inbred lines irrespective of whether these were increasing or decreasing in their effect on time to heading. The values for $H_2/4H_1 < 0{\cdot}25$ indicate unequal frequencies of negative and positive alleles among the parents.

The values for $\frac{1}{2}F/\sqrt{[D(H_1-H_2)]}$ were variable between the diallel sets and in two cases exceeded the theoretical maximum of 1. This expression measures the consistency of the ratio of h to d over all loci.

The quantity $(4DH_1)^{\frac{1}{2}}+F/(4DH_1)^{\frac{1}{2}}-F$ was approximately 0·5 in most cases, indicating that the proportion of dominant and recessive allelomorphs

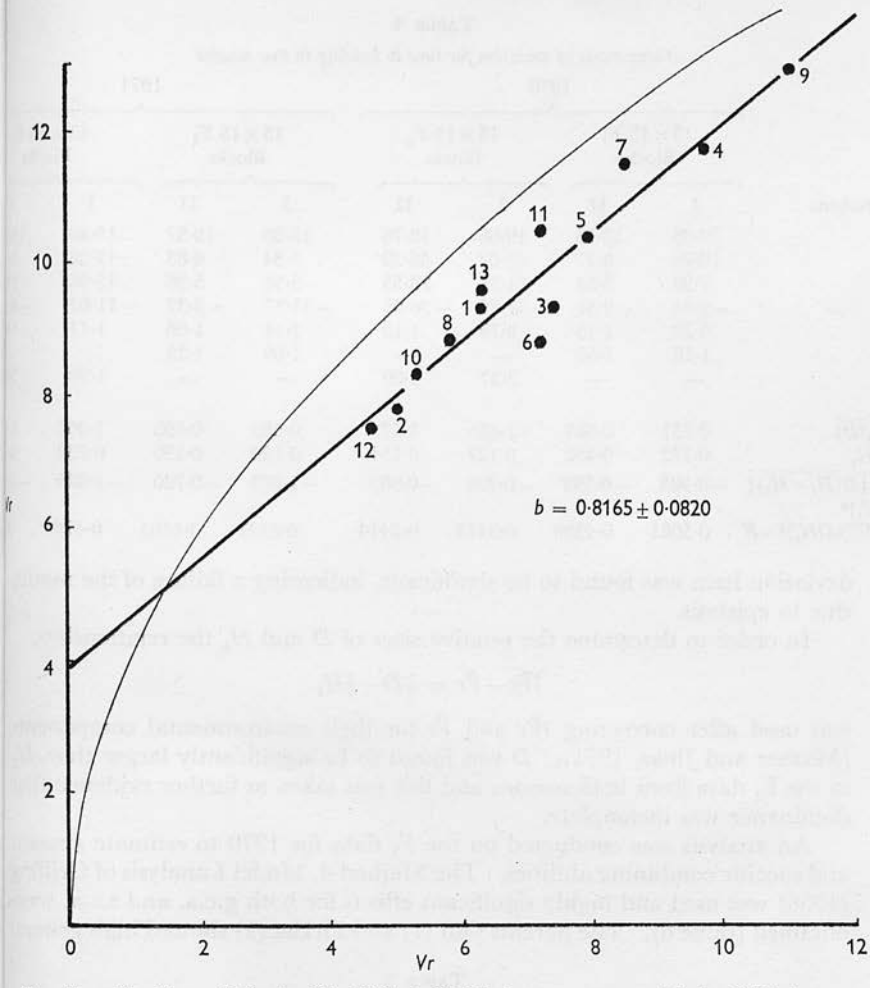

FIG. 4*b*.—*Wr*, *Vr* graph for the 13 × 13 F_2 half-diallel set, means over blocks, 1971 data.

in the parents was unequal and that there were approximately two recessive genes or effective factors for each dominant gene or gene group involved in the control of this character.

More accurate estimates of the genetic components should be obtainable by using more statistics, and 12 are available when F_1 and F_2 data are combined (see Hayman, 1958, tables 1, 1*b*). Seven parameters were estimated (table 5), leaving five degrees of freedom to calculate the variance of the deviations of observed from expected for the 12 statistics. The standard errors in the 1970 results, particularly those associated with H_1 and H_2, were large, but more precise estimates for the components were obtained for the 1971 data. The conclusions drawn from table 4 were largely substantiated.

The values for the seven components derived from the 12 statistics of F_1 and F_2 data pooled were used to reconstruct expected values for the statistics, and the overall deviation of observed from expected was tested against heterogeneity between blocks (Mather and Jinks, 1971). The overall

TABLE 4

Components of variation for time to heading in two seasons

	1970				1971			
	13 × 13 F_1 Blocks		13 × 13 F_2 Blocks		13 × 13 F_1 Blocks		13 × 13 F_2 Blocks	
Component	I	II	I	II	I	II	I	II
D	19·06	18·76	19·06	18·76	15·38	19·32	15·38	19·32
H_1	10·76	8·77	42·02	46·39	5·34	6·85	17·20	4·61
H_2	7·39	5·34	21·34	28·55	3·58	5·36	15·96	2·31
F	−9·34	−9·51	−27·79	−36·05	−11·27	−8·37	−11·61	−6·11
E_0	0·79	1·15	0·79	1·15	1·11	1·05	1·11	1·05
E_1	1·18	1·57	—	—	1·09	1·22	—	—
E_2	—	—	2·57	2·09	—	—	1·96	1·70
$\sqrt{(H_1/D)}$	0·751	0·684	1·485	1·573	0·589	0·595	1·057	0·488
$H_2/4H_1$	0·172	0·152	0·127	0·154	0·168	0·196	0·232	0·125
$\frac{1}{2}F/\sqrt{[D(H_1-H_2)]}$	−0·583	−0·593	−0·700	−0·985	−1·083	−0·780	−1·329	−0·458
$(4DH_1)^{\frac{1}{2}}$ $+F/(4DH_1)^{\frac{1}{2}}-F$	0·5081	0·4590	0·3413	0·2414	0·2332	0·4665	0·4739	0·511

deviation item was found to be significant, indicating a failure of the model due to epistasis.

In order to determine the relative sizes of D and H_1 the relationship,

$$\bar{W}r - \bar{V}r = \tfrac{1}{4}D - \tfrac{1}{4}H_1$$

was used after correcting $\bar{W}r$ and $\bar{V}r$ for their environmental components (Mather and Jinks, 1971). D was found to be significantly larger than H_1 in the F_1 data from both seasons and this was taken as further evidence that dominance was incomplete.

An analysis was conducted on the F_1 data for 1970 to estimate general and specific combining abilities. The Method 4, Model I analysis of Griffing (1956) was used and highly significant effects for both g.c.a. and s.c.a. were obtained (table 6). The parents Olli (1) and Pirkka (2) showed high general

TABLE 5

Components of variation for time to heading calculated from statistics derived from the L_1 and L_2 generations (Hayman, 1958)

	1970 Blocks		1971 Blocks	
Component	I	II	I	II
D	19·6022 ± 2·6438	19·4131 ± 3·4781	15·4484 ± 1·1422	19·3113 ± 0·9383
H_1	11·0664 ± 10·6567	9·7873 ± 14·0197	7·4419 ± 4·6041	8·4106 ± 3·7823
H_2	8·6660 ± 10·4307	9·2192 ± 13·7224	2·7526 ± 4·5065	4·0984 ± 3·7021
F	−13·1666 ± 7·1466	−16·0443 ± 9·4019	−8·5715 ± 3·0877	−5·5229 ± 2·5365
E_0	0·5358 ± 1·8738	0·8559 ± 2·4651	1·0823 ± 0·8096	1·0472 ± 0·6651
E_1	0·5805 ± 1·7284	0·5218 ± 2·2739	1·1490 ± 0·7468	1·3866 ± 0·6135
E_2	4·4808 ± 1·4115	4·5170 ± 1·8570	2·4455 ± 0·6098	1·6229 ± 0·5010
$\sqrt{(H_1/D)}$	0·7514	0·7100	0·5459	0·6599
$H_2/4H_1$	0·1958	0·2355	0·0925	0·1218
$\frac{1}{2}F/\sqrt{[D(H_1-H_2)]}$	−0·9597	−2·4156	−0·5035	−0·3029
$(4DH_1)^{\frac{1}{2}}$ $+F/(4DH_1)^{\frac{1}{2}}-F$	0·3822	0·2642	0·4289	0·6438

TABLE 6

General and specific combining ability effects for time to heading, F_1 data SCA 1970 and 1971 (below) estimates

	2	3	4	5	6	7	8	9	10	11	12	13	GCA 1970	GCA 1971
1	1·811	−0·426	−0·598	1·165	−0·153	−1·262	−0·744	0·747	−1·898	0·665	0·638	0·056	−6·896	−7·190
	1·721	1·030	−0·179	0·703	0·348	0·703	0·939	0·130	−6·142	0·839	−0·070	−0·024		
2		−1·144	−2·917	−0·853	0·029	−2·080	1·438	0·529	−0·317	−0·553	1·020	3·038	−3·178	−2·980
		0·021	−1·188	−1·006	0·239	0·094	0·230	0·321	−0·552	−1·170	0·921	0·367		
3			−0·753	2·311	2·093	−1·317	0·702	−1·808	0·347	−0·189	1·483	−1·298	0·059	0·211
			0·121	2·203	−0·752	−1·397	−0·161	−1·170	−0·642	−0·961	0·930	0·776		
4				−1·062	0·920	0·411	−0·171	0·020	2·274	1·038	0·211	0·629	1·932	1·420
				−0·306	−0·061	−0·106	−0·470	0·121	1·849	0·630	0·321	−0·733		
5					1·883	−1·926	−2·108	0·083	0·838	0·502	−0·426	−0·408	−0·532	0·638
					0·621	0·076	−1·488	1·003	0·330	−1·188	−1·497	0·549		
6	1970 population mean ($\hat{u}$) = 56·7 ± 0·09					0·056	−1·026	0·665	−3·680	0·183	−1·344	0·374	−0·414	−0·108
	S.E. ($\hat{S}_{ij}$) = 0·74					1·121	−1·342	1·049	−0·724	0·358	−0·152	−0·706		
7							1·765	0·656	4·511	−0·326	1·347	−1·835	−2·005	−2·162
							3·112	−1·797	0·330	−0·288	−1·197	−0·652		
8	1971 $\hat{u}$ = 60·3 ± 0·09							−0·326	−1·771	1·193	0·265	0·783	1·977	1·701
	S.E. ($\hat{S}_{ij}$) = 0·69							−1·861	−0·333	1·649	0·439	−0·715		
9									0·620	−1·217	−1·344	1·374	−0·414	1·111
									2·458	−0·161	−0·170	0·076		
10										1·438	−1·089	−1·271	4·532	3·683
										0·667	1·058	1·703		
11											−1·026	−1·708	0·468	−0·199
											−0·161	−0·215		
12												0·265	0·795	1·111
												−0·424		
13													3·677	2·765
S.E. ($\hat{g}_i - \hat{g}_i$)													± 0·35	± 0·32

combining ability for earliness and the largest specific combining ability effect was for Midas × O.A.C. 21 (10 × 7). In order to obtain unbiased estimates the parents were not included in the analysis.

When the analysis was conducted on the 1971 data a very similar result was obtained with regard to general combining ability estimates. Specific combining ability effects were, however, small with the exception of that for the cross Olli × Midas which was as early as the Olli parent.

4. Discussion

The experiment was a large one in terms of the number of genotypes included and the design differs from those of most previously reported experiments on cereals. In these previous experiments, genotypes were grown in plots of several plants within each replication, often with plants widely spaced (Whitehouse *et al.*, 1958; Lupton, 1961; Crumpacker and Allard, 1962; Paroda and Hayes, 1971). In the experiments reported here, plants were grown as closely as possible, commensurate with field recording, so that characters were measured under growing conditions approaching those of agricultural practice. The randomisation of plants within a single block ensured a wide sampling of environmental variability while possible effects of interplant competition were also distributed at random. Replicate blocks constituted statistically independent experiments. The incorporation of parents F_1 and F_2 together in both years permitted comparisons to be made between generations without confounding seasonal effects and the extra statistics obtainable by consideration of the L_1 and L_2 tables together (Hayman 1958, table 1*b*) allowed standard errors to be attached to the estimates of genetic components.

The analysis of variance clearly demonstrated that the genetic variation was largely additive (*a*), and smaller, but nevertheless significant, effects due to non-additive variance were also detected. In the 9 × 9 full diallels in both seasons this non-additive variance fell mostly into the (b_3) category with only a suggestion of gene asymmetry (b_2). In the half diallels significant non-additive effects could be associated with all three (*b*) items. An important assumption in the theory of diallel analysis, namely that of no reciprocal differences, was also tested by Hayman's (*c*) and (*d*) in full diallels. No significant effects were found.

Heterogeneity of $Wr - Vr$ in the graphical analysis was detected in several cases and the regression of Wr on Vr was, in a number of cases, significantly less than unity. In addition, regressions of $W'r$ on Wr indicated asymmetry of gene distribution, associated particularly with the two-rowed genotypes. Whenever possible, interactions were removed and the analysis continued.

In the six-rowed genotypes subgroup, interpretation was relatively straightforward. Dominance was in the direction of earliness, with the point representing the array of Olli, the earliest variety, taking up a position on the regression slope signifying an excess of dominant genes, while in the array of O.A.C. 21 an excess of recessive genes was indicated. This latter result agrees with the findings of Aksel and Johnson (1961). However, when two-rowed and six-rowed genotypes were considered together, O.A.C. 21 was revealed to be relatively early so that the direction of dominance was no longer clear. In addition, when the two-rowed genotype subgroup and the complete diallels were considered, the model was clearly inadequate in

several cases, with regression coefficients significantly less than unity. Ambidirectional dominance was suggested. Three of the four six-rowed parents are adapted to American growing conditions and strong selection may have been practised for time of heading. This may have resulted in the fixation of dominant genes acting in the direction of earliness. In European genotypes, on the other hand, selection has tended towards intermediate or late types, a situation in which different genes, with dominance working in either direction, could survive in the population.

The data for Midas appeared to be largely responsible for failure of the Wr/Vr test, particularly in the 1970 season, although the C-scaling test did not indicate consistent interaction in this array. Nevertheless, considerable improvement in the fit to the model was found when these data were omitted from the analysis. There would thus appear to be evidence for non-independence of gene distribution and the scatter of points in fig. 4*a*, where the point for the Midas array occupies an extreme position, shows curvature which is concave downwards suggesting gene association (Coughtrey and Mather, 1970).

An indication of seasonal effects in the expression of dominance was the clear unidirectional dominance found in the 12×12 diallel (Midas omitted) in the 1971 data. Unidirectional dominance could not be shown in the 1970 data except for the six-rowed subgroup. Paroda and Hayes (1971) also noted changes in the expression of dominance in different environments, and indeed, between two of the eight environments they studied, a complete reversal in the direction of dominance was detected.

The graphical analyses confirmed that in addition to additive effects, partial dominance was operating in the determination of heading time.

Estimation of the components of genetic variation confirmed that D was large relative to H_1 and H_2 in most cases and that F was large and negative, showing an excess of recessive alleles. The precision of the estimates of H_1 and H_2 was low and it is a feature of the set of statistics used that the C-matrix derived from the matrix of coefficients contains relatively large values for the CH_1H_1 and CH_2H_2 elements. In the population as a whole it was estimated that an approximately 2 : 1 ratio existed between recessive and dominant genes for this character. The ratio $\frac{1}{2}F/\sqrt{[D(H_1-H_2)]}$ twice exceeded the theoretical maximum of 1 and in these data was not a useful measure of the consistency of the ratio h to d effects.

The combining ability analyses are perhaps most helpful when making parental choices. High g.c.a. would be desirable if the additive effect of a single genotype was all that was required. On the other hand, if other factors were important in the choice of parents, high s.c.a. for the character analysed, between parents satisfactory in other respects, would be looked for.

The g.c.a. effects in the 1970 and 1971 seasons were highly correlated ($r = 0{\cdot}9692$, $P < 0{\cdot}001$), showing that the additive genetic effects did not interact with seasonal effects. Large negative g.c.a. effects were exhibited by Olli, Pirkka and O.A.C. 21, while Midas and Boreham Warrior showed large positive g.c.a. effects. Estimates for s.c.a. effects in the 1971 season were low, as was the correlation between seasons ($r = 0{\cdot}4005$, $P < 0{\cdot}01$), suggesting that non-additive effects are influenced by environment. The s.c.a. values contain effects due to non-additive variation which may include non-allelic interaction. The variability of s.c.a. effects in the Midas array for the 1970 season is perhaps a confirmation of the disturbances indicated

by other tests. The Boreham Warrior array, on the other hand, showed a much smaller range of values indicating mainly additive effects for lateness in this genotype.

5. Summary

1. Diallel analysis was applied to untransformed data from two seasons for time to heading in spring barley.

2. Analysis of variance of data from 9×9 full diallels at F_1 for two seasons indicated no significant differences between reciprocal crosses. Large additive effects were detected, but non-additive variation was also significant in the control of this character.

3. Analysis of data from 13×13 half diallels at F_1 and F_2 for two seasons also detected significant additive and non-additive effects. Graphical analysis revealed considerable departures from the model which in some cases could be removed by omitting the Midas array from the analysis.

4. No interaction was evident when a subgroup, consisting of a 4×4 diallel between six-rowed parental genotypes, was analysed, and graphical analysis revealed partial dominance with dominance acting in the direction of earliness.

5. Considerable interaction was present when a subgroup, consisting of a 9×9 diallel between two-rowed parental genotypes, was analysed and results were inconsistent over both blocks and seasons.

6. Estimation of genetic components confirmed that additive genetic variance was high and that partial dominance was operating in the inheritance of this character. Gene asymmetry was detected and there was an excess of recessive genes.

7. The expression and direction of dominance was in some cases found to be different between seasons.

8. Large effects for general and specific combining ability both for early and late heading were detected.

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6. References

AKSEL, R., AND JOHNSON, L. P. V. 1961. Genetic studies on sowing-to-heading and heading-to-ripening periods in barley and their relation to yield and yield components. *Can. J. Genet. Cytol., 3,* 242-259.

COUGHTREY, A., AND MATHER, K. 1970. Interaction and gene association and dispersion in diallel crosses where gene frequencies are unequal. *Heredity, 25,* 79-88.

CRUMPACKER, D. W., AND ALLARD, R. W. 1962. A diallel cross analysis of heading date in wheat. *Hilgardia, 32,* 275-318.

EUNUS, A. M. 1964. Inheritance of earliness in barley. *Euphytica, 13,* 49-56.

GRIFFING, J. B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. *Austral. Jour. Biol. Sc., 9,* 463-493.

HAYMAN, B. I. 1954*a*. The analysis of variance of diallel tables. *Biometrics, 10,* 235-244.

HAYMAN, B. I. 1954*b*. The theory and analysis of diallel crosses. *Genetics, 39,* 789-809.

HAYMAN, B. I. 1958. The theory and analysis of diallel crosses II. *Genetics, 43,* 63-85.

JINKS, J. L., AND HAYMAN, B. I. 1953. The analysis of diallel crosses. *Maize Genetics Newsletter, 27,* 48-54.

JINKS, J. L. 1954. The analysis of continuous variation in a diallel cross of *Nicotiana rustica* varieties. *Genetics, 39*, 767-788.

JINKS, J. L. 1956. The F_2 and backcross generations from a set of diallel crosses. *Heredity, 10*, 1-30.

JOHNSON, L. P. V., AND PAUL, G. I. 1958. Inheritance of earliness in barley. *Can. J. Plant Sci., 38*, 219-233.

JONES, R. M. 1965. Analysis of variance of the half diallel table. *Heredity, 20*, 117-121.

LUPTON, F. G. H. 1961. Studies in the breeding of self-pollinating cereals. Further studies in crop prediction. *Euphytica, 10*, 209-224.

MATHER, K. 1949. *Biometrical Genetics*. Methuen & Co., London.

MATHER, K., AND JINKS, J. L. 1971. *Biometrical Genetics*. Chapman and Hall, London.

MATHER, K., AND VINES, A. 1952. The inheritance of height and flowering time in a cross of *Nicotiana rustica*. *Quantitative Inheritance* (ed. E. C. R. Reeve and C. H. Waddington), 49-80. H.M.S.O., London.

NILAN, R. A. 1964. The cytology and genetics of barley 1951-1962. *Monographic Suppl. No. 3. Research Studies*. Washington State University.

PARODA, R. S., AND HAYES, J. D. 1971. An investigation of genotype-environment interactions for rate of ear emergence in spring barley. *Heredity, 26*, 157-175.

SMITH, L. 1951. Cytology and genetics of barley. *Bot. Rev., 17*, 133-335.

WHITEHOUSE, R. N. H., THOMPSON, J. B., AND RIBEIRO, M. A. M. DE V. 1958. Studies on the breeding of self-pollinated cereals. 2. The use of a diallel cross analysis in yield prediction. *Euphytica, 7*, 147-169.

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